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Predatory versatility and intraspecific interactions of *Cyrba algerina* and *Cyrba ocellata*, web-invading spartaeine jumping spiders (Araneae: Salticidae)

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Abstract This is the first behavioural study of *Cyrba ocellata* and an extension of an earlier study of *Cyrba algerina*. *Cyrba* is a spartaeine genus, Spartaeinae being a primitive salticid subfamily. *Cyrba's* behaviour is compared to that of other spartaeines and discussed in relation to salticid evolution. *Cyrba* builds a web-like resting structure which is more or less intermediate between the spacious prey-catching webs of some spartaeines and the compact enclosing nests typical of advanced salticids. In common with some other spartaeines, *Cyrba* is an araneophagic web-invading aggressive mimic that also practises kleptoparasitism and oophagy in invaded webs, and cursorial insectivory away from webs. *C. algerina* and *C. ocellata* have similar behaviour during intraspecific interactions. Also, these species' displays have basic similarities to displays of other salticids except that quiver swim waving is a distinctive display unique to *Cyrba*.

Keywords spider; Salticidae; Spartaeinae; *Cyrba*; predation; aggressive mimicry; display; courtship; mating

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INTRODUCTION

All jumping spiders (Salticidae) have complex eyes and acute vision, and the eyes of these spiders set them apart from all other spiders. Recent comparative studies are providing potential insights into how these unique spiders evolved. Most salticids are exclusively cursorial; they often build tube-like silk nests, but not prey-catching webs. *Portia*, however, is a genus of behaviourally complex and aberrant salticids from tropical Africa, Asia, and Australasia. Five of the eight species of *Portia* have been studied in detail, and all are now known not only to catch prey cursorially but also to build large prey-catching webs, invade alien webs, use aggressive mimicry to catch resident spiders in alien webs, and take eggs and insects from alien webs (Jackson & Blest 1982; Jackson & Hallas 1986a, b).

Along with another 12 genera, *Portia* belongs to the subfamily Spartaeinae, which is characterised by primitive morphology (Wanless 1984a). That most spartaeines have large, functional posterior medial eyes (PME's) is especially noteworthy because most other salticids have vestigal PME's. More remarkably, spartaeines have less well-organised retinal ultrastructure than typical salticids. When considered in detail this can be seen to form a grade between the typical salticid eye and the eyes of nonsalticid spiders (Blest 1985).

The behaviour, morphology, and taxonomy of *Portia* suggested that the Salticidae might have evolved from web-building and web-invading ancestors (Jackson & Blest 1982). This hypothesis became the impetus for comparative study of the behaviour of other spartaeine genera. We now know that, besides *Portia*, two species of *Spartaeus* build large prey-catching webs (Jackson & Pollard 1990) and, besides *Portia*, the spartaeines *Brettus adonis*, *B. cingulatus*, *Cyrba algerina*, and *Gelotia* sp. n. invade alien webs and catch other spiders by using aggressive mimicry (Jackson & Hallas 1986c; Jackson unpubl. data). A review of these recent studies is in preparation.

This paper presents new information on the behaviour of *Cyrba*. *Cyrba* is of particular interest because Wanless (1984b) suggested that it is, phylogenetically, the closest relative of *Portia*. Also, *Cyrba* is the most widely distributed spartaeine genus (Wanless 1984b). Three of the seven species of *Cyrba* are restricted to the tropics; *C. bimaculata* and *C. boveyi* are widespread in Central Africa and *C. legendrei* are known only from Madagascar and the Comoro Islands. *C. lineata* and *C. nigrimana* extend out of the tropics in South Africa. *C. algerina* is distributed widely outside the tropics, being known from the Canary Islands, North Africa, Southern Europe, the Middle East, the U.S.S.R., and the Himalayan Region of India. *C. ocellata* is the most widely-distributed species in the genus: tropical Australia, Southeast Asia from the Philippines to Java, the Indian subcontinent, the U.S.S.R., and East Africa.

The previous behavioural study of *C. algerina* (Jackson & Hallas 1986c) was entirely laboratory-based, the specimens used having been sent to my laboratory from Portugal and France. This paper extends the earlier study of *C. algerina* by presenting new information, from both the field and the laboratory, on this species and *C. ocellata*. This is the first behavioural study of *C. ocellata*.

MATERIALS AND METHODS

Laboratory cultures of *C. algerina* were set up in Christchurch from specimens I collected in Portugal (Sao Blas) and Spain (Granada and Ronda), about 20 specimens from each site. Cultures of *C. ocellata* originated from about 6 specimens sent to me from Thailand by Christa Deelemann and specimens I collected myself: 4 from Australia (Katherine, Northern Territory), 3 from Kenya (Nairobi National Park), and about 30 from Sri Lanka (Mahiyangana). I also observed and collected six juvenile *Cyrba* in Tsavo West National Park in Kenya. Although definite identifications of juveniles are not possible and none of these juveniles lived to maturity in the laboratory, they were probably *C. ocellata*.

The cultures of *C. algerina* originating from Spain (Granada) and *C. ocellata* originating from Sri Lanka provided a large number of specimens for this study. Data from these cultures are presented here. Spiders from the other cultures were studied in less detail but they were very similar, if not identical, in behaviour to the spiders from the primary cultures of each species.

Terminology, conventions for describing behaviour, and the testing and maintenance procedures were essentially the same as in other studies (Jackson & Hallas 1986a). This included the convention that expressions such as "usually" or "generally", "sometimes" or "occasionally", and "infrequently" or "rarely" were used to indicate frequencies of occurrence of c. 80% or more, 20–80%, and 20% or less, respectively.

Whenever possible, *C. ocellata's* behaviour is described by comparing it to previously described behaviour of *C. algerina*, without repeating details that can be found elsewhere (Jackson & Hallas 1986c). Also, whenever possible, only new findings on *C. algerina's* behaviour will be presented in detail. Because *C. algerina* and *C. ocellata* were found to have many similarities in behaviour, the expression "*Cyrba*" will be used whenever pooled data is accurate for both species.

OBSERVATIONS

Habitat

Each study site was in open woodland in xeric areas. The ground was generally very rocky and *Cyrba* was usually found either under rocks or, less often, walking about on the ground or the tops of rocks.

Moulting platforms, egg sacs, and nests

Cyrba spun a small (about twice the spider's body length in diameter), horizontal platform on which to moult. This platform was either flush against or, at most, 1–2 mm below the substrate (i.e., rock or side of cage).

To make an egg sac, *Cyrba* spun a thick silk sheet against the side of a rock—or the side of its cage in the laboratory—then oviposited on the centre of the sheet and covered the eggs with a second, flimsier layer of silk close against the eggs.

Cyrba egg sacs had characteristic clusters of white spots (1 mm or less in diameter) on the outer silk layer. These spots were small tufts of very densely woven silk embedded in the structural silk of the egg sac.

Cyrba generally remained with its eggs, spending much of its time standing on the egg sac but also moving away to catch prey, then returning. Sometimes *Cyrba* remained with uncovered egg sacs. More often, a sparse array of threads was suspended over the egg sac and the spiders stood under this. Also, there was usually a flimsy array of silk around the platform when *Cyrba* moulted, although the spider sometimes moulted on an exposed platform.

A *Cyrba* that was not brooding eggs or moulting might also spin an array of silk to stand under at night and other times when resting. The silk array *Cyrba* spun is called a "nest", but it had little resemblance to typical salticid nests. Very few *C. algerina* nests were seen in the earlier study and the difficulty of discerning the structure of these nests was noted (Jackson & Hallas 1986c). Despite seeing more nests in the laboratory and examining them more closely in this study, it is still difficult to say much about their structure.

Usually, the nest seemed to be no more than an unstructured array of silk above the spider. Sometimes, it was denser and could be described as a flimsy flat sheet of silk suspended over the spider. Occasionally, there was enough silk under and to the sides of the spider to give the nest a more or less enclosing, crudely tubular, structure—something which might have passed for a typical salticid nest if it has been more densely woven.

Nests tended to be only slightly larger than the spider, although they were occasionally as much as two to three times larger than this. It was nests with egg sacs that were most often larger and more structured.

At least in the laboratory, *Cyrba* usually did not bother to build a nest when moulting or simply resting. It usually spent the night simply standing in a secluded place, such as beside one of the corks in its cage or beneath leaf litter or other debris I put in its cage. How common nests were in nature was uncertain because it was difficult to see nests without turning over rocks, and the flimsy nests built by *Cyrba* were probably destroyed when rocks were overturned. Despite these problems, however, a few nests were seen in nature and they were very similar to the nests *Cyrba* built in the laboratory. Also, consistent with laboratory observations, most nests seen in nature were over egg sacs.

Locomotion away from webs

Cyrba's style of locomotion was unique. It stepped forward in a stop-go gait and often ran off suddenly in a different direction without an apparent stimulus. It only rarely leapt. The spider often waved its palps up and down while stepping, but rarely while standing. *Cyrba* might also wave legs I up and down while stepping, but *Cyrba* had another unique way of waving its legs while walking—"swim waving".

When swim waving, *Cyrba* moved its forelegs up and to the side then, without pausing, more slowly down and inward, making contact with and moving 1 mm or more across the substrate. At the end of the down-inward motion, the tarsi were either about parallel to each other and pointing forward or they converged, sometimes so strongly that their tips touched. During the up-and-to-the-side motion, the legs appeared to be loosely elevated, but legs straightened and appeared to stiffen during the down-inward motion.

Sometimes only legs I swim waved. More often, legs I and II swim waved together, legs II moving in matching phase just to the sides of legs I. Sometimes, leg I (or I and II) on one side waved, with leg II (or I and II) on the other side not waving. More often corresponding legs on each side waved.

Cyrba also bobbed its abdomen up and down while stepping and during the pauses between its steps. The abdomen was usually held tilted up from the cephalothorax during bobbing and it moved up and down about an axis intersecting the cephalothorax at 10–20°. Movement of a bobbing abdomen appeared smooth and continuous.

Predation on web spiders

Cyrba readily invaded varied types of webs and preyed on resident spiders. Typically, *Cyrba* oriented toward the web then approached, becoming steadily slower as it got closer, and finally moving very slowly onto the silk. It then became inactive for several minutes before beginning to pluck with its palps. Also, *Cyrba* sometimes twitched its abdomen briefly soon after contacting a web.

There were three modal forms of plucking: up and down, forward and backward, rotary forward and backward. Each modal form, however, varied greatly over short time spans in specific characteristics such as velocity and amplitude. The spider also switched frequently from one modal form of plucking to another. Bouts of plucking were sometimes long and continuous but most lasted only 2–4 s and were followed by a pause of variable length (often many minutes) before plucking was resumed. Occasionally, a spider plucked with just one palp, but it usually plucked with both palps simultaneously. The same modal form of plucking was usually adopted by the two palps, but velocities, amplitudes, and phasing of the two palps often differed considerably.

By plucking, *Cyrba* sometimes lured in the resident spider and, if the resident spider came to within a few millimetres, *Cyrba* attacked by lunging. To lunge, *Cyrba* first slowly lifted legs I and II and extended them forward; then, by propelling itself rapidly forward, *Cyrba* brought its legs over and either stabbed or grasped the prey, which became paralysed within c. 20 s. Stabbed spiders ran away; *Cyrba* watched, then slowly approached and retrieved its paralysed victim.

Cyrba did not readily move completely into webs. Often *Cyrba* remained for prolonged periods (e.g., 2–7 h) on the edge of the web, plucking occasionally and keeping legs IV, at least, on a non-silk substrate (e.g., a twig at the edge of the web). Eventually, if the web spider failed to approach, *Cyrba* sometimes moved slowly farther out into the web and advanced very slowly, eventually coming to within a few millimetres of its victim and making a lunging attack. *Cyrba* usually moved exceedingly slowly when walking or shifting the positions of legs while in contact with, or even just near, webs.

Cyrba sometimes leapt (usually no more than a few body lengths) into webs onto prey, although leaping was less common than attacks by lunging. Leaps were most common when a web spider became inactive after being lured to within 10–30 mm after a long period (e.g., 1 h) of intermittent plucking.

Kleptoparasitism and oophagy

Cyrba only occasionally fed on insects caught in other spiders' webs. It might leap from 2–3 body lengths away onto the insect in the web, but *Cyrba* more often walked across the web to the insect, moving at about the same speed with which it approached spiders on webs. Instead of lunging, it usually attacked when close by simply walking over the insect and inserting its fangs.

Cyrba occasionally ate eggs in webs, but never the eggs of cursorial spiders. To do so, *Cyrba* oriented then walked directly to eggs from 20–50 mm away. Using its chelicerae to grasp the egg sac, *Cyrba* fed on the egg mass as an entity, in much the same way as it fed on a spider or insect.

Locomotion on webs

Cyrba walked with apparent ease on each type of web with which it was tested and stuck to neither cribellate nor ecribellate sticky webs. On webs with widely-spaced threads, *Cyrba* made rotary probes with its forelegs, as has been described for *Portia* (Jackson & Blest 1982).

Cursorial predation on insects

Cyrba readily stalked insects, when away from webs, by approaching rapidly, then slowing down when close and either leaping from 1–3 body lengths away or continuing to approach and lunging from a few millimetres away.

The insect sometimes decamped before the spider attacked and sometimes the spider attacked and missed; the spider never chased the insect. The spider rarely waved palps or legs as it approached.

Sometimes *Cyrba* crouched (lowered its body close to the substrate) before leaping or lunging. Generally, *Cyrba* did not crouch until within 1–3 body lengths of its prey. It might continue to approach slowly while crouched. Sometimes it stood, body crouched, for as long as 20 s before attacking its prey—or before its prey moved away.

Predation on cursorial spiders

Cyrba did not respond to nests of cursorial spiders, regardless of whether they were vacant or occupied, but *Cyrba* did sometimes respond to cursorial spiders away from nests in the same way that it responded to insects. *Cyrba* captured a few small clubionids, but salticids always detected the approaching *Cyrba* and decamped before being captured. *Cyrba* never pursued cursorial spiders very persistently.

Elements of behaviour during intraspecific interactions

1. Twitch abdomen. A spider twitched its abdomen by moving it rapidly up and down. The abdomen paused slightly before each change of direction and bout durations were highly variable, although usually 1–10 s. There was a side-to-side rocking motion superimposed on the basic up-and-down motion.

2. Erect legs. When legs were erect there was usually distinct flexion at the femur-patella joints but, from the patella, the remainder of each leg was fully extended at each joint and appeared stiff. There were four modal positions in which spiders held legs erect.

Femora of legs in Position 1 extended somewhat upward but, from the femur-patella joints to the tarsi, these legs extended either about straight forward or slightly up and to the side.

In Position 2, femora were moved up and back, and the rest of the leg inward so that legs converged from the patellae to form a "V" with the tips of the tarsi (the narrow end of the "V") close together if not actually touching. From the femur-patella joints to the tarsi, Position 1 and 2 legs were anywhere from c. 20° up to c. 20° down, sometimes touching the substrate.

In Position 3, the spider held the femora of their erect legs pulled far back and angled up but, in contrast to Position 2, with femur-patella joints only moderately flexed so that tarsi angled up and to the side c. 45°.

In Position 4, erect legs were held out sharply to the sides of the body (about perpendicular to the sagittal plane of the body) with all joints being more or less fully extended. Usually, Position 4 erect legs were held about parallel to the substrate; occasionally they pointed up 20–45°.

It was generally legs I that spiders held erect. Often, one or both legs II were also erect, held parallel and lateral to legs I, but legs II were always returned to the substrate when the spider was stepping. Sometimes spiders displayed briefly with legs I and II in different positions: legs I in Position 1, legs II in Position 3; legs I in Position 3, legs II in Position 4. Occasionally, contralateral legs were in different positions (Positions 1 and 3 or 3 and 4) or only one leg of a pair was erect (any position), but both contralateral legs were usually held erect in matching positions.

Although both sexes, in all types of intraspecific interactions, sometimes displayed with legs in erect Position 2, this display was most commonly performed by males interacting with females. Females held their legs erect in Position 2 (the "V" posture) only very briefly and infrequently.

3. Semi-erect legs. Unlike erect legs, semi-erect legs were not quite fully extended from patellae to tarsi. They appeared to be loosely elevated. Semi-erect legs were held in Position 1 or 3, but not Position 2 or 4.

4. Hunched legs. Legs I–III were held out about perpendicular to the sides of the body, legs I and II being highly flexed. Tarsi I and sometimes II were held just off the substrate, but tarsi III remained on the substrate. Legs II were not always hunched and were sometimes erect while legs I were hunched, or they might remain in the normal posture on the substrate.

5. Posturing. While either walking or standing, the spider postured by holding its hunched (hunched posturing), erect (erect posturing), or semi-erect (semi-erect posturing) legs more or less stationary.

6. Erect, semi-erect, and hunched waving. Hunched, erect, or semi-erect legs waved by moving up and down two or three times at large amplitude. If legs III were hunched, erect, or semi-erect, they were generally waved at the same time as legs I. Erect and semi-erect legs were never waved in Positions 2 or 4.

7. Erect palps. *Forward* erect palps were similar to forward erect legs: distinct flexion at femur-patella joints; rest of palp fully extended and positioned about parallel to the substrate or angling down as much as 45°. The spider held erect palps parallel to each other or converging somewhat, sometimes with tarsi touching or crossing over.

Downward erect palps extended down perpendicular to, or as much as 20° forward from perpendicular to, the substrate. Usually all joints, including femur-patella joints, were fully extended. The two palps were parallel to each other or they converged somewhat, but tips of the tarsi generally stayed at least 0.5 mm apart. Generally, the spider's cephalothorax was raised when its palps were downward erect.

8. Other palp postures. Palps in the *normal* posture hung loosely in front of the chelicerae. Femora of palps in the *lateral* posture angled up and to the side, with the rest of each palp angling down and to the side. Femora of *raised* palps angled nearly vertically upward, with the rest of each palp angling straight down beside chelicerae.

9. Palp flutter. The spider fluttered its palps by waving them up and down very rapidly 2–5 times.

10. Spurt. A male spurted by advancing rapidly toward a female in a rapid stop-and-go manner with his body lowered close to the substrate. Although legs were usually erect, they sometimes remained on the substrate and stepped. Even when stepping, however, the male's legs maintained a posture similar to the erect posture (often including a "V" configuration). Sometimes the male waved erect legs as he stepped, and he sometimes moved along an arc with each advance, reversing direction with each successive advance, thereby progressing forward on an interrupted zigzag or spiral path.

11. Step-to-side. The male stepped to his left (or right) with legs erect, paused, then stepped to his right (or left), then stopped for a few seconds before stepping-to-side again. As a male walked to his left, his right legs I and II were brought down onto the substrate to step, but left legs I and II remained on the substrate; legs reversed roles when the male reversed direction.

12. Dance. Males danced, when interacting with females, by stepping in a special way while facing the female and either erect posturing or erect waving, although one leg I might be lowered to step. Erect legs were always in Position 1 or 2. *C. algerina* performed five types of dancing but *C. ocellata* performed only two of these—zigzag and linear.

13. Zigzag dance. A zigzag dancing male stepped to one side, paused for a few seconds, stepped to the other side, and so forth.

14. Linear dance. To linear dance, a male stepped forward then immediately back. With or without pausing first, he might step forward and back several more times. The male's erect legs I often moved inward and upward as he stepped forward and then back to their original position as he stepped backward.

15. Semicircular dance. A male performed semicircular dances by moving forward in a straight line, then back on an arc.

16. Elliptical dance. A male performed elliptical dances by looping forward to the left (or right) then looping back to the right (or left).

17. Complex dance. A male combined zigzag, linear, semicircular, and elliptical dances in various ways to perform complex dances.

18. Sway. Spiders, with legs erect (Position 4) or hunched, swayed by moving their bodies from side to side without stepping. If swaying with erect legs, the spider often brought right legs I and II down to the substrate while moving left, and vice versa while moving right. When brought down to the substrate, legs I and II stayed erect but moved forward some.

Only *C. ocellata* swayed with legs hunched. Often flexion of hunched legs was less during swaying than during hunched posturing, and usually the flexion of the spider's legs changed (increased, decreased, or both) slowly while the spider swayed. A spider might slowly switch back and forth between erect and hunched posturing. When swaying with hunched legs, the spider usually held its cephalothorax higher above the substrate than normal, with abdomen tilted down. The spider's abdomen was usually tilted in the opposite direction from how its cephalothorax was moving while swaying with legs hunched.

Spiders swaying with legs erect often kept their cephalothoraces and abdomens aligned and did not raise their bodies.

19. Embrace. Embracing spiders stood face-to-face with legs I and II erect, out to the side and extending up 20–45°. While embracing, the two spiders' tarsi I and, sometimes II, touched, and the spiders sometimes moved closer together and brought their faces into contact. Often, spiders had their chelicerae spread apart, with fangs extending down, while embracing.

20. Grapple and push. A spider grappled, while embracing, by moving legs I and II over the other spider's legs or body and flexing them repeatedly so as to pull on the other spider. One or both embracing spiders pushed by attempting to step forward and one spider was sometimes forced backwards 1–10 mm. Spiders often grappled and pushed at the same time.

21. Bent abdomen. A bent abdomen was tilted 20–45° to the left or right of the cephalothorax. Spiders often had their abdomens bent (usually away from the direction of movement) while posturing, swaying, or stepping to the side with legs erect in Position 4 or hunched.

22. Strike. Only *C. algerina* females struck, and they did so only when interacting with males. To strike, the female raised legs I then very rapidly and forcefully brought them down and forward onto the male or onto the substrate in front of the male.

23. Charge. A female charged by suddenly running toward a male and stopping before making contact. Usually, she charged three to six times in rapid succession. Unlike spurting males, charging females did not hold their legs elevated, nor did they lower their bodies.

24. Truncated leaps. Males, while erect (Position 3 or 4) or hunched posturing, made truncated leaps by suddenly lowering their legs and leaping 2–3 mm toward, but failing to make contact with, another male no more than 10 mm away.

25. Long leaps. This display consisted of one spider suddenly leaping toward the other spider, making contact or landing close by, then immediately running away.

26. Lunge. A spider lunged by moving its body suddenly and rapidly forward, somewhat similarly to how it lunged to catch prey. Spiders lunging during intraspecific interactions, however, generally did not open their chelicerae, nor did they slowly elevate their forelegs, before moving forward, and they did not scoop up the target object with their legs. Instead, the spider moved its body forward, sometimes contacting the other spider face-on, then immediately moved back to its original position.

27. Ram. A female rammed a male by making a series of short charges or truncated leaps and contacting the male head on at the end of the last leap or charge. Alternatively, the last charge or leap was followed immediately by a lunge that brought about contact. Only *C. algerina* did this.

28. Propulsive displays. Striking, charging, truncated leaping, long leaping, lunging, and ramming were termed "propulsive displays".

29. Quiver legs. A spider quivered legs by moving them very rapidly at low amplitude (c. 10/s, 0.5 mm). Only legs I and II were quivered. Only males performed this behaviour and only when interacting with females.

30. Quiver swim wave. This was the same as swim waving except that legs quivered during the down inward part of each cycle of waving, which was especially slow. Only legs I or, occasionally, I and II quiver swim waved.

31. Ordinary premount tapping. While standing in front of the female, a male performed ordinary premount tapping by moving legs I and II up and down against the female, without quivering the legs.

32. Mount. Males mounted females by walking over them and, usually, immediately veering toward one side.

33. Quiver tapping. A male tapped a female by quivering legs I or, usually, legs I and II while holding these legs over the female so that tarsi touched the female's dorsal abdomen, carapace, or legs.

When *premount quiver tapping*, a male stood in front of a female with legs extended over the female as when performing ordinary premount tapping. Quivering legs might or might not be erect and, if erect, might be in Position 1 or 2.

Mounted and facing the opposite direction from the female, the male *postmount quiver tapped* by quivering legs I and II so that his tarsi I and II repeatedly struck or rubbed across the side of the female. The female's abdomen might gradually rotate while the male tapped.

34. Stroke. If the female's abdomen began to rotate while the male quiver tapped, the male brought his opposite leg I over and stroked by moving his tarsus repeatedly across the female's ventral abdomen. If the female's abdomen did not begin to rotate while the male quiver tapped, the male first stroked with his nearer leg I then, if the female's abdomen rotated, switched to stroking with the opposite leg I.

35. Quiver palps. A spider quivered its palps while holding them in the rest posture or after lowering them somewhat from this position. Sometimes the spider lowered its palps far enough so that tarsi were on the substrate or, if the quivering spider was a male mounted on a female, the female's body during quivering.

Quivering palps appeared to move similarly to quivering legs (c. 10/s, 0.5–1.0 mm, primarily femoral movement). Movement seemed to be primarily, but not exclusively, up and down. Bout lengths were extremely variable (c. 1 s to c. 1 min). Palp quivering might be performed alone while the spider stood or walked, or it might be performed while the spider erect postured in Position 1 or 2, danced, spurted, stepped to the side, premount tapped, or abdomen twitched. It was very often performed at the same time as leg quivering, and was often in conjunction with quiver swim waving and quiver tapping.

36. Ordinary palpate and quiver palpate. Often when a male walked over portions of the substrate on which a female had been standing earlier, or when he walked on silk on or near a female's nest, he performed ordinary palpating by moving his palps side to side across the substrate or the silk.

The male quiver palpated by quivering his palps at the same time as he palpated. He might simply quiver palpate or he might alternate between ordinary and quiver palpating.

Sequences of behaviour during intraspecific interactions

Behaviours performed by each species and sex, and the types of interactions in which they were performed, are indicated in Table 1. Typical sequences of behaviour are described below.

Successful tests (definition: tests in which interactions took place) were more difficult to stage at nests than away from nests (Table 2) because the nest resident tended to leave the nest before the intruder arrived; the test was terminated when this happened. Also, successful tests seemed to be easier to stage with male-female pairs than with male-male or female-female pairs.

The duration of interactions was similar for both species and for interactions at and away from nests, but male-female interactions tended to be much longer than intrasexual interactions (Table 3).

Male-female interactions

A male faced a female, from as far as 100 mm away, erected his legs, and began to approach. *C. ocellata* males sometimes displayed initially with hunched legs and switched to erect legs soon afterwards, but hunched legs displays by males were not a regular feature of male-female interactions of either species. The male often spurted toward the female early in the interaction; stepping-to-side and dancing predominated later.

C. ocellata, but not *C. algerina*, males often began by posturing in erect Position 3 or 4, switching to Position 1 and 2 posturing as they approached the female. *C. algerina* males usually postured in Position 1 and 2 from the beginning.

A consistent pattern usually developed for *C. algerina*. The male, in rapid succession, twitched his abdomen, fluttered his palps, waved his erect legs, then stepped-to-side or briefly danced. The male then stood, erect posturing for a few seconds, before repeating this sequence. *C. ocellata* sometimes performed sequences like this also, but this was not a regular behaviour of *C. ocellata* males.

When the male placed one or both tarsi on the substrate while dancing, stepping-to-side, spurting, or simply walking, he often kept them in a "V" configuration, and they made few, if any, stepping movements.

When distant from the female, the male tended to display with erect legs in Position 1, shifting them to Position 2 as he got closer. Sometimes, especially if the male was within a few millimetres of the female, femora of legs in Position 2 were drawn far back (almost 90° to the side and up as much as 45°), and tarsi often crossed over.

When legs I were in erect Position 1, legs II were sometimes extended forward; they remained on the substrate, while extending under and, often, in front of legs I. Legs III were angled forward too, but less distinctly than legs II.

Cyrba algerina males quivered their legs primarily during quiver swim waving and quiver tapping.

Table 1 Behaviours performed by each species and each sex, and the types of interactions in which they were performed. CA = *C. algerina*; CO = *C. ocellata*.

	Male-female	Female-male	Male-male	Female-female
Palp fluttering	CA,CO	X	CA,CO	X
Postmount quiver tapping	CA,CO	X	X	X
Premount quiver tapping	CA*,CO	X	X	X
Quiver legs without swim waving	CA*,CO	X	X	X
Quiver palpating	CA,CO	X	X	X
Quiver swim waving	CA,CO	X	X	X
Ramming	X	CA	X	CA
Semi-erect posturing Position 1	X	CA,CO	X	CA, CO
Semi-erect posturing Position 3	X	CA,CO	X	CA,CO
Semi-erect waving	X	CA,CO	X	CA,CO
Spurting	CA,CO	X	X	X
Stepping-to-side	CA,CO	X	X	X
Striking	X	CA,CO	X	X
Stroking	CA,CO	X	X	X
Swaying	X	CO	CA,CO	X
Truncated leaping	X	CA,CO	CA,CO	CO
Twitching abdomen	CA,CO	CA,CO	CA,CO	CA,CO

*Rare

Table 2 Test results.

		Cyrba algerina		*Cyrba ocellata*	
		At nest	Away from nest	At nest	Away from nest
Male-female	No. of tests	22	30	23	32
	Interaction*	73%	90%	61%	94%
	Mating**	9%	17%	9%	25%
Male-male	No. of tests	18	26	17	24
	Interaction*	44%	85%	35%	92%
Female-female	No. of tests	18	28	16	28
	Interaction*	50%	89%	37%	72%

*Percentage of tests in which spiders interacted
**Percentage of tests in which spiders mated

Besides quiver swim waving and quiver tapping, *C. ocellata* also quivered legs while posturing with legs in erect Position 1 or 2, both while standing and walking. *C. algerina* also did this, but only rarely. *C. ocellata* sometimes quivered legs that were on the substrate, extended forward more than normal, but not erect. *C. algerina* did this only very rarely.

Cyrba algerina rarely quivered its legs for more than c. 1 s at a time, even if it was quiver swim waving or quiver tapping. *C. ocellata*, however, often quiver swim waved or just quivered legs in bouts of 2–5 s and occasionally for as long as c. 30 s at a time.

Males, but not females, fluttered their palps. Fluttering was seen most often in conjunction with dancing and stepping-to-the-side, the male usually fluttering just before or as he began stepping.

The female usually spent most of her time during the interaction simply watching the male and intermittently decamping. When she decamped, the male usually watched and followed, often keeping legs erect and sometimes spurting along behind the female, and the female stopped and watched the displaying male several more times before the interaction ended. Females twitched their abdomens intermittently and occasionally postured or waved with legs hunched, erect, or semi-erect.

At seemingly unpredictable intervals, females performed propulsive displays, especially if the male was only 10–20 mm away, after which the male usually backed away with legs erect. The female often turned and ran away from the male.

Cyrba ocellata females sometimes walked toward males and initiated embraces. The female's legs were hunched or erect (Position 4) as she advanced, and the male moved his legs to erect Position 4 as the female approached or just after she made contact.

Table 3 Interaction durations. Pooled data for *Cyrba algerina* and *Cyrba ocellata*, and for interactions at and away from nests.

	N	Median	Range
Male-female	86	2.5 min	0.25–15 min
Male-male	58	0.5 min	0.25–6 min
Female-female	60	10 s	5–90 s

If the female persisted in decamping, embracing, or performing propulsive displays, the male eventually stopped approaching and the interaction ended.

In about half the interactions, males failed to get close enough to females to extend legs over them. Males mounted females in only about one-third of the interactions in which they got their legs over females, but the pair mated in every interaction in which the male mounted.

Cyrba algerina usually approached females with legs erect, extended erect legs over the female and began to perform ordinary premount tapping with legs still erect. They only occasionally quiver tapped before starting to perform ordinary premount tapping. *C. algerina* might continue ordinary premount tapping for as long as 15 s before attempting to mount, but it usually relaxed its legs, so that they were no longer erect, almost as soon as ordinary premount tapping began.

Typically, before mounting, a *C. ocellata* male extended erect legs over a female and premount quiver tapped, then performed ordinary premount tapping. A *C. ocellata* male might or might not begin premount ordinary tapping with legs erect, but it always relaxed these legs before mounting.

Cyrba algerina males never premount quiver tapped for more than c. 2 s, but *C. ocellata* sometimes premount quiver tapped for as long as 10 s at a time and there could be several bouts before *C. ocellata* mounted. Also, *C. algerina* males never kept legs erect while over females for longer than c. 5 s, but *C. ocellata's* legs remained erect while over females for as long as 20 s.

Cyrba ocellata males often extended erect legs and quivered them over females without quiver tapping (i.e., without legs touching the female). Usually, they soon lowered their legs—erect or not—and premount quiver tapped, but they sometimes immediately began ordinary premount

Table 4 Data from copulations observed in the laboratory. Pooled data for *Cyrba algerina* and *Cyrba ocellata* and for matings at and away from nests.

	Duration of copulation	Duration of individual palp applications	No. of palp applications
Mean	41 s	26 s	1.6
SD	15.5 s	12.7 s	0.51
N	17	27	17

tapping, then mounted. *C. algerina* males were not observed to quiver legs over females without tapping.

After mounting a female, males of both species began postmount quiver tapping.

Copulation

Copulation was always brief and consisted of only one or two palp engagements (Table 4). Copulation always ended when the female became active and began walking or running away with the male's palp still engaged. The male fell off the decamping female and did not resume courtship, although he might briefly watch and follow her. While copulating, the male and female faced in opposite directions, with the male dorsal (mating posture 2: Gerhardt & Kaestner 1938).

Intrasexual interactions

Interactions usually began when spiders faced each other as far as 70 mm (females) or 110 mm (males) apart, and erect (Position 3 or 4) or hunched postured. However, females occasionally began interactions by erect posturing in Position 1 or semi-erect posturing in Position 1 or 3, or by performing propulsive displays.

Generally, spiders hunched postured more when within 20 mm of each other but erect postured (Position 3 or 4) more when further away. Spiders occasionally erect postured in Position 1 or semi-erect postured in Position 1 or 3, but only briefly. Spiders occasionally erect and hunched waved and performed propulsive displays. Males and females twitched their abdomens and males might flutter their palps, sway, or embrace. A common pattern was for a spider to stand posturing with legs hunched, then extend its legs out in erect Position 4 as it stepped forward, backward or to the side a few millimetres and return its legs to the hunched posture when it stopped stepping c. 1 s later.

Palp postures

Cyrba algerina was not seen displaying with erect palps, but both sexes of *C. ocellata* in all types of interactions sometimes held palps erect. When posturing or swaying with legs erect, in Position 3 or 4, or hunched, *C. ocellata* held palps erect, lateral, or raised. Lateral and raised were more common if a spider was less than two body lengths from the other spider; erect was more common if it was further away.

Generally, when a spider postured or swayed, it held its palps downward erect if its cephalothorax was raised and its legs were hunched, but held its palps forward erect if its cephalothorax was not raised and its legs were erect. Occasionally, a spider held palps forward erect and legs erect in Position 3 or 4 with cephalothorax raised; however, even if its cephalothorax was raised, a spider more often had its palps forward erect when its legs were erect in Position 3 and 4.

Interactions in the presence of nests

Nests had little effect on interactions. Nests were so thin and their openings so spacious that spiders on the two sides of the silk displayed in much the same way as they did when there was no nest present. When males walked onto females' nests, however, they usually twitched their abdomens and quivered their legs and palps, usually with leg and palp tarsi touching the silk. These spiders, however, usually soon had their attention attracted by movements of the other spider and began erect posturing or dancing.

Cohabitation

Nine cohabiting pairs (adult male with subadult female) were seen in nature: three *C. algerina* (Spain), and six *C. ocellata* (Sri Lanka). Two of the *C. algerina* and one of the *C. ocellata* males were under the silk in the nest with the female, but the locations of the other six males were uncertain.

In the laboratory, when males were put in cages with nests occupied by subadult females, they displayed as in interactions with adult females, then took up residence beside or in the nest. Three *C. algerina* and four *C. ocellata* pairs stayed together until after the female matured 2–6 days later. During this time, each pair was checked intermittently. The female was always in the nest; the male was usually outside, but close to, the nest.

DISCUSSION

Spinning behaviour

Portia and *Spartaeus* build large prey-capture webs (Jackson & Hallas 1986a; Jackson & Pollard 1990), but *Cyrba* builds only small web-like arrays of silk with no evident role in prey capture. *Spartaeus*' web is a large dense sheet on tree trunks. *Portia* builds two types of webs: Type 1, a small horizontal sheet suspended well away from the substrate; Type 2, a large three-dimensional array with a crudely funnel-like shape. Although *Cyrba* is not a web-building salticid, its spinning behaviour has interesting similarities to that of *Portia* and *Spartaeus*, and can almost be envisaged as a link to the nest building of typical salticids. *Cyrba's* three-dimensional arrays do not have the funnel-like shape of *Portia's* type 2 webs but do have the appearance of small, rudimentary webs. Sometimes *Cyrba* makes a small sheet and, although not large and dense like *Spartaeus'* web, this sheet is not so unlike a Type 1 web of *Portia* except that *Cyrba*, unlike *Portia*, places the sheet near the substrate. At other times, *Cyrba* makes a more enclosing, somewhat tube-like array of silk with a crude resemblance to a typical salticid nest. *Cyrba* seems to have, in its spinning behaviour, the rudiments of building space webs, sheet webs, and tubular nests

Egg sacs

Portia usually places its egg sac on a dead leaf suspended in a web (Jackson & Hallas 1986a). *Cyrba* and *Brettus* (Jackson & Hallas 1986c) place their egg sacs on the substrate, but the egg sacs of these three spartaeine genera are otherwise remarkably similar: eggs on a thick silk sheet covered by a thin sheet on which there are scattered dense flecks of silk that give the egg sac a characteristic spotted appearance. No salticids other than these three spartaeine genera are known to build this type of egg sac.

Normal locomotion away from webs

Portia has a slow, choppy style of locomotion, very different from that of *Cyrba*. *Cyrba's* rapid stop-and-go gait is more similar to the agile walking of typical salticids and, among spartaeines, it most resembles that of *Brettus*. However, no spartaeines studied are quite like typical salticids in how they walk. *Cyrba* and *Brettus*, for example, have an unusual tendency to run for several centimetres, suddenly and spontaneously, then resume walking. There are also special features of *Cyrba's* locomotion. *Cyrba*, but no other spartaeines studied, bobs its abdomen while, and during pauses between, stepping. A few non-spartaeine salticids are known to bob their abdomens similarly—*Cosmophasis micarioides*, *Natta* (= *Cyllobelus*) *rufopictus*, and Myrmarachne spp. (Jackson, 1986a, b, c). It was suggested (Jackson & Hallas 1986c) that *Cyrba's* abdomen bobbing functions in ventilation, but why only this genus among studied spartaeines might ventilate in this fashion is unclear.

Swim waving is the most distinctive aspect of *Cyrba's* mode of locomotion and this behaviour seems to be unique to *Cyrba*, although the way *Brettus* waves its legs has some similarities (Jackson & Hallas 1986c).

Web invasion and aggressive mimicry

Various species of salticids are known to prey on web spiders by leaping or, less often, walking into webs (Jackson 1986d; Jackson & Macnab 1989). The only salticids known to make specialised vibratory signals (aggressive mimicry) and to have the ability to walk with ease on diverse types of webs, including cribellate and sticky ecribellate webs, are certain spartaeines—*Gelotia* sp. n (Jackson unpubl. data), five species of *Portia* (Jackson & Hallas 1986a), two species of *Brettus* (Jackson & Hallas 1986c), and two species of *Cyrba*. The behaviours used by these different spartaeines to make vibratory signals are remarkably similar, although *Portia's* repertoire is much the largest. The behaviours of *Gelotia*, *Brettus*, and *Cyrba* are, more or less, subsets of *Portia's* repertoire.

Oophagy, kleptoparasitism, and cursorial predation

Cyrba feeds not only on the spiders it finds in alien webs but also insects found in the spider's web and the spider's eggs. These modes of feeding, oophagy and kleptoparasitism, are also practised by *Portia*, *Brettus*, and *Gelotia* (Jackson 1986a, c, unpubl. data), and by a few web-invading non-spartaeine salticids (Jackson 1986d). All of the web-invading spartaeines that have been studied also are, like typical salticids, cursorial predators of insects. *Portia*, however, is considerably less efficient at cursorial predation on insects than at catching spiders in webs (Jackson & Hallas 1986b). *Brettus*, *Gelotia*, and *Cyrba*, in contrast to *Portia*, are competent cursorial predators of insects (Jackson 1986c, unpubl. data).

Portia fimbriata from Queensland, but no other populations of this species or any other studied species of *Portia*, uses a specialised behaviour called "cryptic stalking"—as a special tactic for very efficiently preying on cursorial salticids (Jackson & Hallas 1986b). In the present study, I found no evidence of anything like cryptic stalking when *Cyrba* was given access to salticids as prey, and *Cyrba* never succeeded at catching salticids in the laboratory.

The Queensland *Portia fimbriata* also takes cursorial salticids—and other cursorial spiders belonging to other families—and their eggs from their nests and uses specialised behaviour for doing this (Jackson & Hallas 1986a). These behaviours are not known for other spartaeines, although a few non-spartaeine salticids take spider eggs from alien nests (Jackson 1986d, unpubl. data). In this study, there was no evidence of these behaviours when I gave *Cyrba* access to alien nests.

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Predatory versatility and intraspecific interactions of *Supunna picta* (Araneae: Clubionidae)

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Abstract Unlike most clubionids, which are nocturnal, drab coloured, hunting spiders, *Supunna picta* is a highly active diurnal spider with distinctive markings. How this spider interacts with prey and conspecifics was investigated, and the evolutionary significance of this unusual spider's behaviour is discussed. *S. picta* is shown to be a versatile predator which not only catches prey cursorially; it also builds a web it uses for detecting prey and invades alien webs where it catches insects and the resident spiders. Unlike some web-invading spiders from other families, *S. picta* does not use aggressive mimicry when in alien webs. *S. picta* has a very rapid, erratic style of locomotion which seems to be important in both prey capture and in escape from its own predators. During intraspecific interactions, *S. picta* performs distinct display behaviours, interactions at and away from webs being similar. Males cohabit with subadult females in webs and mate after they mature. Females make flat, papery egg sacs, more like the egg sacs of many gnaphosid spiders than the typical egg sacs of clubionids.

Keywords spider; *Supunna picta*; Clubionidae; predation; courtship; communication

INTRODUCTION

The Clubionidae is one of the largest families of spiders. They are generally envisaged as drab-coloured nocturnal hunting spiders with poorly developed vision (Bristowe 1941) and are sometimes called "sac spiders" (Bristowe 1958) because they make densely-woven tubular nests. *Supunna picta* (L. Koch) is strikingly coloured for a clubionid and, in fact, one of the most distinctive spiders in the New Zealand fauna. This recent introduction from Australia (Forster & Blest 1979) is now found commonly in New Zealand around houses and in open country with short grass cover. As a clubionid, it is unusual because it can be seen moving about actively in the daytime. This paper is the first detailed study of the predatory behaviour and intraspecific interactions of *S. picta*. We show that *S. picta* is, besides being a hunting spider which catches prey without the use of a web, also a web-builder and a web-invader.

MATERIALS AND METHODS

Laboratory studies were carried out using juveniles (body length 2–7 mm) and adults of both sexes. Adult males and females were similar in body length (c. 8 mm). Spiders were collected from Christchurch and Kaikoura (South Island, New Zealand). We frequently collected *S. picta* that we saw active out in the open, e.g., around human habitations and along road cuttings. In Kaikoura, spiders were observed and collected in Kowhai Bush, part of the Marlborough Catchment Board Kowhai River Protection Reserve, where they were found in their webs beneath stones in a partially overgrown stream bed. Field data was collected in Kowhai Bush on two occasions (15–16 November 1986 and 17–18 February 1987): each *S. picta* egg sac found was collected; before collecting it, the presence or absence of a web, spider, or both was noted.

In the laboratory, "tents" were sometimes placed in cages to encourage web-building: 70 × 70 mm pieces of black card taped to the floor of the cage and

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arched up to create a 10–20 mm high space underneath. Otherwise, maintenance, testing, terminology and conventions for describing behaviours were as described elsewhere (Jackson & Hallas 1986a). This included the convention that expressions such as "usually" or "generally", "sometimes" or "occasionally", and "infrequently" or "rarely" were used to indicate frequencies of occurrence of c. 80% or more, 20–80%, and 20% or less, respectively.

Potential prey were introduced to the cage containing the *S. picta*. In these tests, *S. picta* sometimes had a web, but the web never filled the entire cage. Prey-capture sequences away from and from within the web were called "cursorial" and "web-based" predation, respectively. Prey used were: fruitflies, *Drosophila melanogaster* (Meigen); houseflies, *Musca domestica* (Linnaeus); ants, *Chelaner antarctica* (White); and salticid spiders, *Marpissa marina* Goyen, *Trite auricoma* (Urquhart), *T. planiceps* Simon, and *Euophrys parvula* Bryant. The salticids and houseflies were similar in size to the *S. picta*, whereas the fruitflies were considerably smaller. The salticids used were species from the same habitats as *S. picta* in New Zealand.

To observe interactions of *S. picta* with web spiders, a clean transparent cage was attached to a similar cage containing a web spider in its web (we filling the cage) to create one large cage half fille with web. *S. picta* was introduced to the clean side o the compound cage.

Although all spider silk is probably adhesive t some extent (Hallas & Jackson 1986), some spider enhance the stickiness of structural lines in thei webs by adding special substances ("glue"). Cribellat spiders add bands of extremely fine fibres. Ecribellat spiders may build non-sticky webs (i.e., withou "glue") or add droplets of sticky fluid, to make ecribellate sticky webs. We tested *S. picta* with web-building spiders of each type: non-sticky, cribellate sticky, and ecribellate sticky (Table 1). All of these spiders are species that are sympatric with *S. picta* in New Zealand and Queensland. *Argyrodes antipodiana* is a kleptoparasitic spider that normally lives in association with other web-building spiders; in tests using this species, the host spider was removed.

BEHAVIOUR AND NATURAL HISTORY

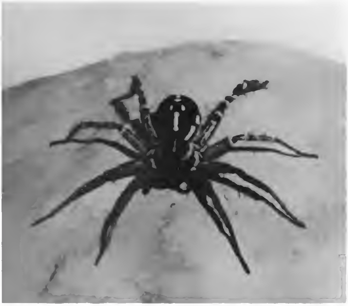
Rest Posture

At rest (Fig. 1, 2), *S. picta* remained stationary with its body close to the substrate and legs extended.

Table 1 Results from testing *Supunna picta* with web-building spiders.

Test spider	Family	Web	No. of tests	*S. picta* ate test spider	Test spider ate *S. picta*
Achaeranea sp.[1]	Theridiidae	Ecribellate sticky space web	48	14	5
Araneus pustulosus[1] (Walckenaer)	Araneidae	Ecribellate sticky orb web	18	3	0
Argyrodes antipodiana[2] (O. P. -Cambridge)	Theridiidae	Ecribellate sticky space web fastened to web of *A. postulosus*[3]	8	4	0
Badumna longinquus[1] (L. Koch)	Amaurobiidae	Cribellate sheet web	26	4	2
Cambridgea antipodiana[1] (White)	Stiphidiidae	Non-sticky sheet web	22	5	0
Inola subtilis Davies[1]	Pisauridae	Non-sticky sheet web	24	2	0
Mynoglenes[2] sp.	Linyphiidae	Non-sticky dome web	9	6	0
Pholcus phalangioides[1]	Pholcidae	Non-sticky dome web	12	0	4
Steatoda sp.[1]	Theridiidae	Ecribellate sticky space web	10	1	2
Tegenaria domestica[1] (Clerck)	Agelenidae	Non-sticky sheet web	10	2	0
Zosis genicularis[1]	Uloboridae	Cirbellate orb web	10	0	0

[1] Size (body volume of test spider/volume of *S. picta*) c. 0.5.
[2] Size c. 0.1.
[3] *A. pustulosus* removed before test.


1 *Supunna picta* female in resting posture.

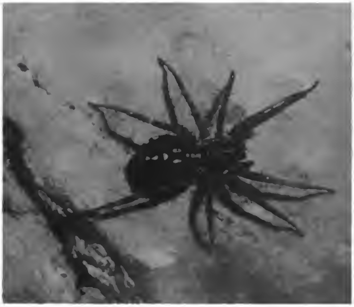


Fig. 2 *Supunna picta* female in resting posture.

ch leg was flexed only slightly. Tibiae I–III were out level with the top of the cephalothorax; tibiae were slightly higher.

When a walking spider stopped, it usually adopted e rest posture by rapidly repositioning each leg 2–3 nes. The spider might also move legs I rapidly up d down 3–6 times (c. 2 mm; c. 5/s), then place em on the substrate before becoming quiescent.

ode of lomotion

upunna picta's mode of locomotion was distinctive it difficult to describe. The spider repeatedly darted vay, stopped briefly, then darted away again. piders running across stones and open ground in ture tended to move for 5–10 s, suddenly pause (in e rest posture) for 10–20 s, then suddenly run gain. While in motion, the spider often executed merous, erratic changes in direction before opping again. When we attempted to capture *S. cta* in nature, its movements became even more pid and erratic. Occasionally, *S. picta* walked ore slowly, often waving legs as it did so by oving them up and down in alternating phase (c. 5 m, c. 5/s, tibial motion).

Vebs

n nature *S. picta* was often found in small non-ticky webs under stones or other objects (Fig. 3). In e laboratory, *S. picta* spun webs in corners of cages r under the cardboard tents provided. Males, emales, and juveniles of all sizes build webs. These vebs were sparse, irregular 3-dimensional arrays; within the array, there was an ill-defined silk tunnel in which the spider usually rested. The tunnel was not delimited by definite sheets of silk, although the web was usually slightly thicker around the tunnel. A typical web of an adult was 50–100 mm across.

A few lines of silk could often be seen to run across the substrate, but these never formed anything like a definite silk sheet and the spider in the web generally stood with its feet directly on the substrate.

Supunna picta moulted and oviposited in its web, in nature, and the laboratory. Exuviae were suspended on lines around the tunnel, but *S. picta* always put its egg sacs on the substrate within the tunnel.

Egg sacs

Supunna picta made a flattened, oval egg sac of papery silk (7–9 mm long, 4–7 mm wide, 2–3 mm thick). It consisted of two thin, but densely spun, sheets of tough, shiny, white silk (Fig. 4) which enclosed a spherical egg mass. In the field, egg sacs were generally positioned within slight indentations under rocks, the lower silk sheet being fastened firmly to the substrate. The lower sheet had a thickened rim and the upper sheet of the egg sac was convexly curved along its length and joined tightly to the rim of the lower sheet. A third layer of silk, which was non-papery and not so dense, covered the egg sac, and this layer usually had foreign matter, such as dirt and prey remains, incorporated into it (Fig. 5).

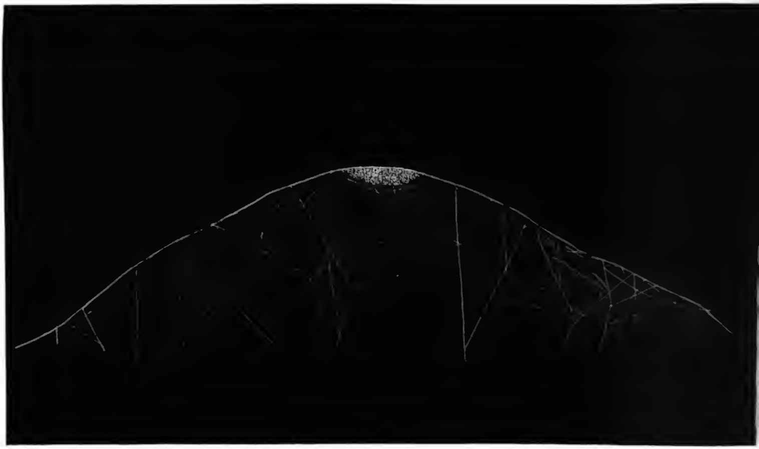


Fig. 3 Drawing of web of *Supunna picta.* Three "tunnels" evident.

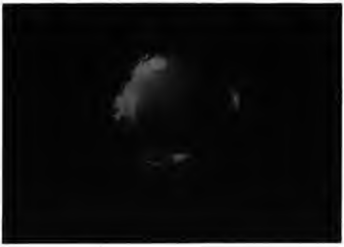


Fig. 4 Egg sac of *Supunna picta,* with web, outer silk covering and detritus removed.

Fig. 5 *Supunna picta* female (on right) standing in web beside egg sac (on left). Compare to Fig. 4. Note non-papery silk over egg sac with embedded detritus.

Most clubionid egg sacs seem to be spherical egg masses placed in nests, wrapped in silk and guarded by females. *S. picta's* egg sac is atypical because it is flattened in shape, made of tough papery silk, attached firmly to the substrate, and covered by a silk jacket with embedded foreign matter. Many gnaphosids make similar egg sacs (Forster & Blest 1979; Jarman & Jackson 1986). Some other spiders are also known to make similar egg sacs, including a few species of salticids (Jackson 1985, 1986b; Wanless 1985).

Supunna picta spiderlings had no evident difficulty leaving these egg sacs when, in the laboratory, the female was removed before the eggs hatched. Egg sacs from which spiderlings had departed had one or more curved slits (2–3 mm long). Presumably the spiderlings left the egg sac through these slits. How these slits were made is unknown.

Egg-sac construction and oviposition

A spider began making an egg sac by putting a thin layer of threads, which was somewhat larger than the eventual egg sac would be, across the substrate. Next, the spider spun a thick outer rim for the sac on this silk layer by moving the tip of its abdomen in a figure eight pattern within a localised region and, intermittently, the spider pivoting c. 180° to spin at the other end of the egg sac. After 30–60 min, the rim was completed. Next, the spider made short strokes of its abdomen across the egg sac for c. 2 min, then oviposited. Oviposition took c. 1 min.

After ovipositing, the female covered the eggs: starting at one end of the egg sac, she swept her abdomen, with large amplitude strokes, back and forth across the eggs as she worked her way to the centre. She then turned c. 180° and spun in the same way from the other end of the egg sac. By repeating this sequence numerous times, the spider put a smooth, shiny layer of silk over the eggs.

After c. 2 h, spinning became slower and the spider started making strokes across the length of the egg sac and onto the substrate. Occasionally, the spider now lifted her abdomen above the egg sac, rather than spinning directly across it. Also, spinning became much more rapid. After c. 5 min of this, the spider stopped spinning and began walking about in the cage. Using her chelicerae, the spider picked up sticks, broken leaves, and other detritus and carried them to the egg sac. Still using her chelicerae, she moved and turned them about until they stuck loosely to the silk. She then firmly fastened these objects down by spinning more silk over them.

After attaching several objects to the silk in this way, the spider spun a second sheet across the egg sac. This sheet was less dense than the first and had a somewhat fluffy appearance. To make this sheet, the female attached threads at various points across the width of the egg sac. Again she started at one end and worked her way towards the centre. However, before reaching the centre each time, she swapped ends, thus creating two fluffy sheets which gradually converged. At frequent intervals, the female stopped spinning, collected more detritus, and fastened it to the two converging sheets. After c. 60 min, the fluffy sheet was complete and the detritus was firmly embedded in it. The spider next spent c. 30 min spinning zigzag patterns of threads across the egg sac, interrupted by periods during which it stopped spinning briefly and either groomed or just remained inactive.

Sperm webs and sperm induction

Male spiders must transfer sperm from their testes to their copulatory organs on their palps before mating. To do so, they make a special web—the sperm web—on which to deposit sperm; then they take the sperm up into their palpal organs from this web, a process called "sperm induction" (see Foelix 1982). Sperm webs are usually either triangular or rectangular, although some spiders make single-line sperm webs. Little seems to be known about sperm webs of clubionids, although Peck & Whitcomb (1970) described the sperm web of *Chiracanthium inclusum* (Hentz): a small rectangular sheet suspended by numerous supporting lines.

Although sperm induction (see Foelix 1982) was not observed, this apparently took place inside the male's web because, on three different occasions in the laboratory, we noticed a "sperm web" suspended within a male's web. The "sperm web" was a thin, semi-opaque, c. 5 × 3 mm rectangular sheet suspended at c. 45°, the lower end being c. 1 mm above the substrate.

The sperm web of *S. picta* was evidently not very different from that of *Chiracanthium inclusum*. The primary difference seems to be where these two species place their sperm webs: *C. inclusum* in a sac like nest; *S. picta* in a web.

Method of attacking prey

Supunna picta attacked by rapidly moving over and, using its chelicerae, seizing the prey. *S. picta* also used legs I to scoop in and hold large prey under the chelicerae and, if the prey was large, *S. picta* used additional legs (sometimes all legs) to hold the prey.

Cursorial predation

Whether darting about or just standing in the open, *S. picta* did not react in any obvious way to potential prey more than 10 mm away. Even if *S. picta* touched or was touched by a potential prey, it might just run away. Sometimes, however, *S. picta* suddenly attacked and captured prey after contact. If it was not facing the prey when contact was made, *S. picta* turned rapidly towards it immediately before attacking. Occasionally, both *S. picta* and its prey were walking within c. 10 mm of each other when *S. picta* suddenly reacted, before contact was made, by turning around and running over the prey. *S. picta* sometimes captured several prey, one after the other, by scooping them into a single food bundle and feeding on them as a unit.

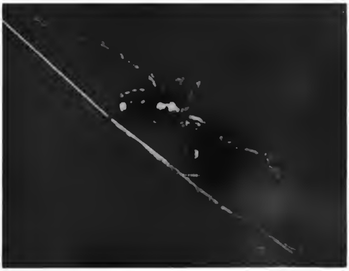


Fig. 6 *Supunna picta* female (facing down and right; side view) walking across web of *Achaearanea* sp., having captured web owner.

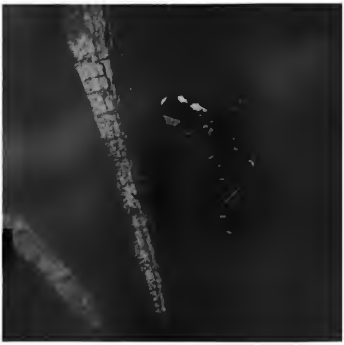


Fig. 7 *Supunna picta* female (facing down) at edge o *Achaearanea* sp. web, eating web owner.

Supunna picta reacted initially to flies, ants, and salticids in the same way, but always released ants soon after contact. This was true in tests off webs and when *S. picta* was in webs (see below).

Predation from own web

Supunna picta normally remained inactive in its web, but usually responded immediately when potential prey contacted the web. *S. picta's* response might be to run out of the web and away. Sometimes it attacked: it rapidly turned as much as 180° towards the prey then moved directly toward it by running across the web or the substrate. *S. picta's* rapid response seemed to be critical in prey capture because its web never restrained prey for long. Often the prey escaped from the web before *S. picta* reached it, but *S. picta* usually ran after and caught it away from the web. While *S. picta* was under or on its web, it moved in a straight line towards the prey but, once away from the web, *S. picta* reverted to its typical zigzag style of running. Soon after capturing it, *S. picta* usually carried its prey back to, and fed in, the web tunnel.

Table 2 Results of testing *Supunna picta* with insects ensnared in webs of other spiders.

Insect	Spider	No. of tests	*S. picta* ate insect
Ctenopseustis sp.[1]	*Badumna longinquus*	22	2
Drosophila melanogaster (Meigen)[2]	*Araneus pustulosus*	15	1
	Badumna longinquus	20	3
	Inola subtilis	25	2
	Zosis genicularis	21	1
Micromus tasmaniae (Walker)[3]	*Badumna longinquus*	18	2
	Inola subtilis	15	1
Musca domestica (Linnaeus)[4]	*Badumna longinquus*	18	1

[1] Tortricid moth (Lepidoptera)
[2] Fruit fly (Diptera)
[3] Lacewing (Neuroptera)
[4] Housefly (Diptera)

Prey capture by web invasion

In the laboratory, *S. picta* sometimes entered all types of webs with which it was tested (Table 1). It walked on twigs and other objects near or within webs, waving legs I as when hunting cursorially, and also walked on the silk (Fig. 6). Sometimes *S. picta* caught and ate the resident spider (Fig. 7; Table 1) or an ensnared insect (Table 2) in the alien web.

Supunna picta sometimes got stuck on webs with glue and, during and after contact with sticky webs, usually spent a great deal of time grooming, especially its legs. Usually *S. picta* freed itself by biting threads and pulling legs away with evident difficulty; sometimes *S. picta* was unable to free itself from sticky webs even after several hours.

If the resident web spider approached, a stuck and struggling *S. picta* usually froze and the web spider left it alone, although *S. picta* was sometimes killed and eaten when it got stuck in these webs (Table 1).

Supunna picta caught web spiders and insects in alien webs in four ways.

1. While *S. picta* was walking in, or at the edge of, the web, the web owner approached; when the web owner got close, *S. picta* attacked and caught it (*N* = 12).
2. While *S. picta* was walking in the web, the web-owner approached. S. *picta* froze, remaining inactive sometimes for more than an hour. The web owner usually stopped when *S. picta* froze, but later began walking about. When the web owner walked close by, *S. picta* attacked and caught it (18).
3. When the web spider (8) or an insect (5) moved, *S. picta* ran across the web to attack it.
4. The web owner or ensnared insect was inactive and *S. picta* was walking in the web. *S. picta* touched, attacked, and caught the web spider (3) or insect (9).

Observations of predation in nature

Once, a *S. picta* female was found in the open eating an unidentified insect, presumably the result of cursorial prey-capture. Another *S. picta* was found in its own web under a stone with the remains of an apparently eaten *Marpissa marina* (Salticidae).

Twice *S. picta* was seen feeding on web spiders: a *S. picta* female beside an *Achaearanea* sp. web, feeding on the apparent web-owner; a *S. picta* juvenile feeding on an *Achaearanea* sp. but not near a web. Prey capture was observed once when a *S. picta* ran under an *Achaearanea* sp. web and, almost immediately, captured the web occupant.

Predatory versatility

Supunna picta is a versatile predator that builds a prey-capture web, catches prey in alien webs, and hunts cursorially. Only cursorial hunting is known for other clubionids (Bristow 1941).

Clubionids are thought generally to be nocturnal hunters which respond to prey, by suddenly seizing it, only after contact. Their eyes are simple (Land 1985) and they rely little, if at all, on visual cues in prey-capture sequences. Also, *S. picta* makes no apparent use of visual cues. When away from webs, *S. picta* resembles typical clubionids by attacking prey only after contact.

Yet, even when acting cursorial, *S. picta* is an unusual clubionid because it is diurnal and appears to be constantly on the go, darting about and relying on speed, rather than stealth, to a much greater extent than seems to be true of other clubionids. The distinctive way in which *S. picta* streaks across open ground may enable this spider to make frequent encounters with potential prey. Erratic, rapid locomotion may also be significant in making this spider a difficult target for its own predators; it was certainly a difficult spider for arachnologists to catch!

The typical sac-like nests of clubionids are sites for resting, moulting, oviposition, and, for at least some species, mating (Pollard & Jackson 1982). The web of *S. picta*, although it serves these same functions, is structurally very different from other clubionids' small, tightly woven nests: it is clearly a web.

Supunna picta's web probably has little significance as a snare. Instead, it seems to act primarily as an extension of the spider's sense organs. Because of its web, *S. picta* perceives nearby animals and acts appropriately. *S. picta* is not unusual for a web spider in this respect. Many spiders build webs that function primarily as extensions of the spider's sense organs, rather than as snares (see Witt 1975). *S. picta* does seem to be an unusual web spider, however, because it readily runs out of the web and across the substrate to catch prey that contact and escape from the web.

Besides being a web builder, *S. picta* is a web invader that sometimes captures and eats insects (kleptoparasitism) and spiders (araneophagy). There has been considerable interest recently in the biology of web-invading spiders. *Argyrodes* spp. (Theridiidae), in particular, are highly proficient specialists at kleptoparasitism (Vollrath 1979).

Argyrodes antipodiana along with *Taieria erebus* (Gnaphosidae), *Pholcus Phalangioides* (Pholcidae), some (perhaps most) species of mimetids, and a few salticids use aggressive mimicry in catching spiders after web invasion (Czajka 1963; Forster & Platnick 1984; Jackson & Hallas 1986a,b; Jackson & Whitehouse 1986; Whitehouse 1986; Jarman & Jackson 1986; Jackson & Brassington 1987).

Supunna picta, however, does not use aggressive mimicry. *S. picta's* success as a web invader seems to depend on speed. The web owner seems to have difficulty escaping from or attacking and catching *S. picta*, because of the rapid, erratic style of *S. picta's* locomotion. *S. picta's* distinctive locomotion might also attract the web spider to *S. picta*: when the web spider rushed out to attack the walking *S. picta*, or a least to investigate the disturbance caused by *S. picta*, *S. picta* sometimes suddenly lunged at and caught the spider. Walking itself might be envisaged as an unspecialised form of aggressive mimicry.

Sometimes the tables were turned and *S. picta* became the victim. *S. picta*, however, had another defence, besides running rapidly and erractically. Sometimes *S. picta* froze (became suddenly quiescent) on the web when the web owner approached. Also, remaining quiescent provided *S. picta* with occasional opportunities to ambush a web owner that came too close.

Supunna picta seemed to be comparatively unspecialised in how it caught insects and spiders on alien webs. No aggressive mimicry was seen and *S. picta* showed no obvious expertise at using stealth. Instead, *S. picta* appeared to practise kleptoparasitism and araneophagy opportunistically.

Intraspecific interactions

The literature may often give the impression that clubionids have little or no courtship. For example, Foelix (1982) states: "Typically, the male simply crawls over the female, pulls the female's abdomen close, and inserts one palpal organ into the female's genital opening". Distinctive tactile and vibratory courtship, however, is now known for three clubionids—*Chiracanthium inclusum* (Peck & Whitcomb 1970), *Clubiona cambridgei* (Pollard & Jackson 1982), and from this study, *S. picta*. We suspect that courtship, although easily overlooked, is well-developed in the Clubionidae.

Elements of behaviour on intraspecific interactions

Lunge. To lunge, the spider suddenly and rapidly thrust its body forward 2–4 mm by extending its rear legs, but it did not leap (i.e., it kept its legs firmly on the substrate). The spider's body always moved back to its original position at the end of the lunge.

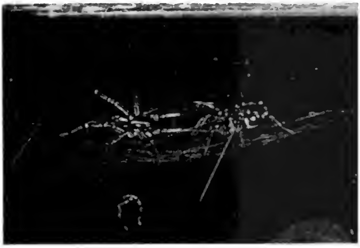


Fig. 8 *Supunna picta* male (left) in web, with legs raised forward and over female's legs, approaching female (right).

Charge. A spider charged by suddenly running 20–100 mm straight toward another spider, then suddenly stopping before making contact. A spider that was charged at usually ran away.

Chase. Two spiders ran 20–200 mm, the chasing spider remaining close behind the chased spider. Often a chase began when one spider suddenly ran toward another, as when charging, but continued running after the other spider when the other spider ran away.

Gape. A spider gaped by standing for 1–60 s with basal segments of chelicerae spread widely apart and fangs extended.

Forward legs posture. Legs I extended parallel to each other in front of the spider (Fig. 8). There was 20–90° flexion at the femur-patella joints and 0–45° at the tibia-metatarsus joints. Generally, legs were less flexed when the spider was still distant from its partner and more flexed when the spider was close enough to have its tarsi over its partner's legs or body.

Raised forward legs. Spiders usually kept forward legs on the substrate while distant from the other spider, but often had them raised, with tarsi over the other spider's legs or body, when close (Fig. 8). Tibiae of raised forward legs were about parallel to the substrate and tarsi were 2–3 mm above the substrate.

Raised lateral legs. Raised lateral legs were held similarly to raised forward except that they angled

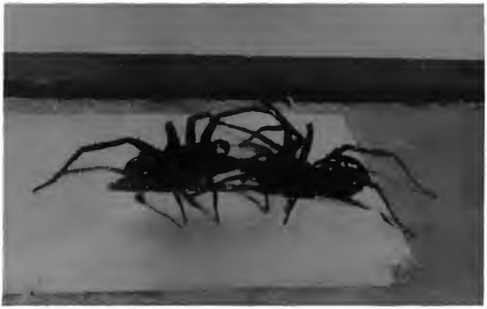


Fig. 9 *Supunna picta* male (left) drums on female's legs. Female (right) has legs raised lateral.

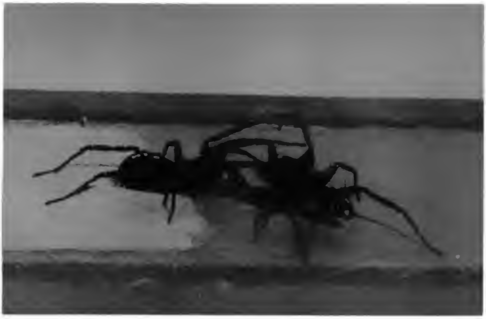


Fig. 10 *Supunna picta* male (right) drums, with legs highly flexed (compare to Fig. 9), on female's legs. Female (left) has legs raised lateral.

out 10–20° to the side, with at least moderate flexion always remaining at the femur-patella and tibia-metatarsus joints (Fig. 9).

Drumming. A spider drummed with palps and forelegs (legs I and II) by moving all six of these appendages at the same time, or the spider might drum with only a subset of these appendages. It never drummed, however, with legs II unless also drumming with legs I, palps, or both. A spider sometimes drummed with a single leg I, but never with a single palp or a single leg II.

A spider usually held its drumming legs more or less in the forward posture (Fig. 10, 11, 12), often highly flexed (Fig. 11), and moved them up and down (10–20/s, alternating phase). Legs moved 3–4 mm and palps moved 2–3 mm. Leg movement was primarily femoral, but palp movement was both femoral and tibial. Tarsi of drumming legs repeatedly contacted the substrate, the other spider or the web during downstrokes. Drumming palps could sometimes be seen to make similar contact, but this usually could not be discerned. When close to another spider, *S. picta* sometimes drummed with legs in more or less the raised lateral posture (Fig. 9, 10).

Laying down silk. To lay down silk, a spider bent its abdomen to one side and touched its spinnerets to the substrate or the silk of another *S. picta's* web. It sometimes made quick, small amplitude, lateral

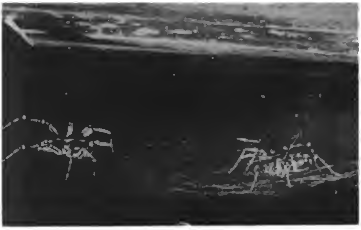


Fig. 11 *Supunna picta* male (left) drums, with legs highly flexed, on female's web. Female (right) in web.

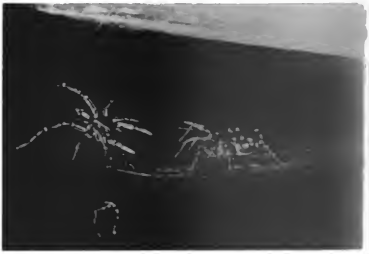


Fig. 12 *Supunna picta* male (left) drums and approaches female (right) in web. Compare to Fig. 11.

movements of the abdomen before walking forward, bending its abdomen to the opposite side and repeating the sequence. By repeating this sequence numerous times, the spider lay zigzag patterns of silk across the substrate, web, or both. A spider laid down silk on another spider by walking over, and placing zigzags of silk on, the other spider.

Abdomen bobbing. In the normal posture, the spider's abdomen is held parallel to the cephalothorax. The spider bobbed its abdomen by raising and lowering it from this position (1–2/s; up 30°, then back to the normal position). Up and down motions were at comparable speed, and these movements had a smooth appearance.

Jerky walking. This mode of walking, although difficult to describe, had a distinctive jerky appearance and it was clearly different from a spider's ordinary locomotion. The spider jerky walked by suddenly darting forward 1–2 body lengths, then pausing 1–2 s before darting forward again, staying in motion only c. 0.2 s or less each time. When jerky walking, *S. picta's* leg movements were apparently of larger amplitude than normal, which caused the spider apparently to move jerkily. Also, during jerky walking, in contrast to normal walking, *S. picta* did not zigzag.

Although normal walking did not cause conspicuous web vibration, webs vibrated conspicuously when *S. picta* jerky walked on them. The spider often drummed, laid down silk, or twitched its abdomen while jerky walking.

Embrace and grapple. Spiders embraced by approaching each other and, just before making contact, raising legs I 45–60° off the substrate in the lateral raised posture. Continuing to advance, the spiders' legs I touched and were pushed back to c. 90° to the sagittal planes of the spiders' bodies. Sometimes spiders advanced still farther and brought their faces together. To grapple, spiders reached over each other with legs I and each spider moved legs I up and down on the other spider's legs (Fig. 13), body, or both. Spiders might just embrace or just grapple, or they might first embrace then almost immediately grapple before separating 1–5 s after contact.

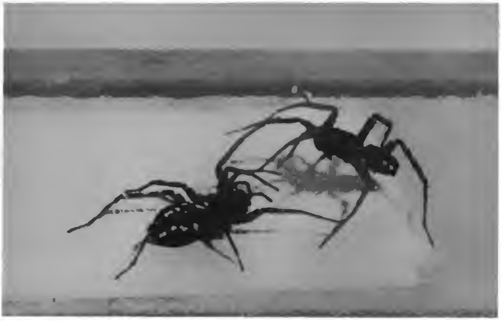
Quiver leg. While in the copulatory position, the male sometimes quivered legs by repeatedly flexing one or both legs IV (2–10/s, c. 1 mm). Movement was tibial and metatarsal. Leg quivering was most noticeable during the first two palpal insertions.

Quiver body. When body quivering, most or all legs quivered as described for legs IV in leg quivering. When body quivering, unlike when leg quivering, the spider stood on the substrate or web and its body moved up and down 1–2 mm. Movement of the spider's abdomen was especially conspicuous.

Copulation. To copulate, the male mounted the female by walking over her (Fig. 14), leaning left (Fig. 15) or right (Fig. 16, 17), and engaging his palp. The male and female faced opposite directions while copulating, with the female's abdomen always rotated 45–90° about its dorso-ventral axis to bring the female's epigynum nearer the male's palp. The female's abdomen sometimes remained parallel to the substrate (Fig. 15) but it usually angled up 20–45° (Fig. 16, 17).

Gerhardt & Kaestner (1938) provided a classification of spider mating postures. According to this classification, *S. picta's* uses Posture 2: male

g. 13 *Supunna picta* male ght) and female (left) begin to apple.



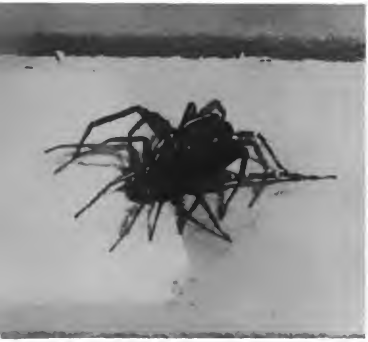


Fig. 14 Male (facing right) walks over female (facing left; body covered by male).

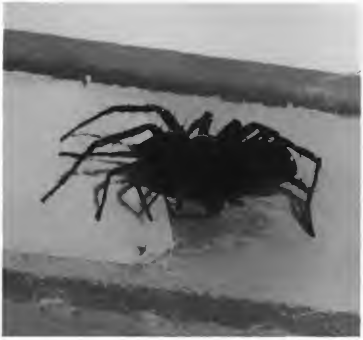


Fig. 15 Male-female pair of *Supunna picta* copulate. Male facing right; female facing left. Male's left palp engaged. Female's abdomen rotated so that ventral side is in view. Female's abdomen not raised.

and female face in opposite directions; male stands over female, his ventral side toward female's dorsal; male applies one palp at a time. Posture 2 is adopted by many other cursorial spiders, including some other clubionids (Pollard & Jackson 1982), but it is an unusual posture for a web-building spider (see Jackson & Hallas 1986a). Interestingly, *Chiracanthium inclusum* adopts a different copulatory posture with little resemblance to the posture adopted by *S. picta* or most other spiders (Peck & Whitcomb 1970).

Convulse. To convulse, the male raised his cepthalothorax slightly then pressed it down towards the female. Simultaneously, he slightly straightened all his legs. The male convulsed during the first insertion of each palp and each convulsion was preceded and succeeded by brief (0.5–1 s) leg quivering.

ORGANISATION OF BEHAVIOUR

An "interaction" was defined as a test in which one or both spiders performed one or more of the behaviours listed in Table 3. Often it was difficult to

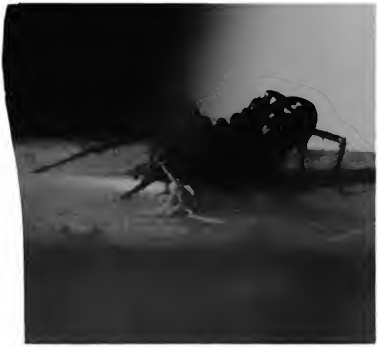


Fig. 16 Male-female pair of *Supunna picta* copulate. Male facing right; female facing left. Male's right palp engaged (behind female's abdomen in photograph). Female's abdomen raised, and rotated so that dorsal side is in view.

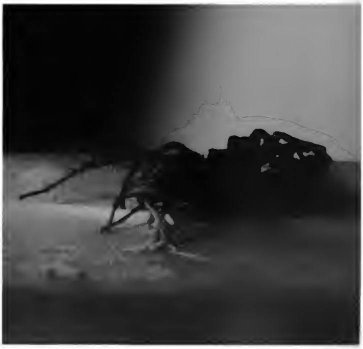


Fig. 17 Male-female pair of *Supunna picta* copulate. Male facing right; female facing left. Male's right palp engaged (behind female's abdomen in photograph). Female's abdomen raised so that dorsal side is in view. Female's abdomen only slightly raised (compare to Fig. 16).

say whether or not spiders did indeed interact and the numbers in Table 4 should be viewed as approximations.

The end of an interaction was defined as when spiders ceased to perform behaviours in Table 3 and moved away from each other. All intrasexual and most intersexual (male-female and male-subadult) interactions lasted only 1–5 s. When interaction failed to occur within 30 min, the test was terminated. Also, if a spider in a web decamped before the other spider contacted its web, the test was terminated unless one spider was displaying.

Male-Female interactions

Interactions in the absence of webs usually began when spiders touched each other, seemingly by accident, and the male immediately began to drum on the female's legs and body. Sometimes, however, a male began to drum while still several body lengths distant from the female. Later in the interaction, the male sometimes bobbed his abdomen, laid down silk, and walked jerkily, and the female sometimes lunged at the male.

When a web was present, interactions usually began when males touched webs and started drumming on the silk. Sometimes, however, interactions began when a male drummed on the substrate before touching the web. Although these males did not walk in a straight line to the web, they usually reached the web within less than 1 min after starting to drum. Soon after the male began to drum, regardless of whether the web had been touched, the male usually began walking about jerkily, intermittently laying down silk and bobbing his abdomen as he did so.

Interactions were distinctly different depending on whether the female had previously mated (Table 5): virgin females always, and previously mated females never, mated during the interaction (Fisher Exact Test, $P = 0.001$). Also, females collected as adults in the field always failed to mate when tested with males in the lab.

If mating did not take place, interactions usually ended when the female decamped and the male failed to follow her. Sometimes, however, interactions ended when females ran toward males. Males always turned and ran away when females ran toward them and most males escaped, but five previously mated females chased down, killed, and ate fleeing males.

Mating was always preceded by characteristic sequences in which the female stayed more or less stationary and the male repeatedly approached and withdrew from her. During each approach, the male usually walked jerkily and drummed, especially with his palps. Sometimes he also laid down silk and twitched his abdomen. The male repeatedly entered and left the web if the female was inside (Fig. 11, 12). Upon reaching the female, the male drummed on her legs I (Fig. 8, 9, 10, 13) and, during successive approaches, he moved farther and farther over her (Fig. 14), often walking right over her and away then approaching again. He often laid down silk on the female when he walked over her. Eventually the male stayed mounted and mated.

Table 3 Behaviours of *Supunna picta* during intraspecific interactions.

	Male-Female	Male-Subadult	Intrasexual
Abdomen bob	M, F	M, S	M, F
Charge	F	S	M, F
Chase	F	S	M, F
Convulse	M	X	X
Drum	M	M	M, F
Embrace	M, F	M, S	M, F
Gape	F	M, S	M, F
Grapple	M, F	M, S	M, F
Jerky walk	M	M	X
Lay down silk on partner	M	M	X
Lunge	F	S	F
Quiver body	M, F	M, S	M, F
Quiver legs	M		

M: performed by male. F: performed by female. S: performed by subadult. X: did not occur.

Occasionally, a male approached a female from the side (Fig. 18) or the rear and drummed. When he did so, the female sometimes briefly raised her abdomen, a leg IV, or both while the male drummed, then the female moved away. However, approaches were usually head on.

The male continued to drum when he walked over the female, first on the female's carapace then on her dorsal abdomen. Before mating, the male leaned from one side to the other to drum on each side of the female's abdomen. The female usually raised her legs when the male drummed on them (Fig. 9, 10, 13) and she eventually rotated her abdomen, enabling the male to engage his palp, when he drummed on the sides of her abdomen.

After engaging one palp, spiders usually moved apart rapidly and, after a brief pause, males resumed sequences of approaching and withdrawing. Males sometimes (N = 11) attempted to change palps without first dismounting, but these attempts were successful only twice.

Clubiona cambridgei males enter females' nests to mate, either by walking through existing doors or by first tearing an opening in the silk (Pollard & Jackson 1982), whereas *Chiracanthium inclusum* females leave their nests and mate on web-like scaffoldings attached to their nests (Peck & Whitcomb 1970). *S. picta* is different from these two species because there is no significant physical barrier between the female and the courting male. *S. picta* males gain access to females simply by walking into their webs.

Table 4 Results of tests for intraspecific interactions of *Supunna picta*.

		Male-Female	Male Subadult	Male-Female Male	Male-Female Female
No web present	No. of tests	51	35	58	65
	No. of tests in which spiders touched each other	38	21	40	45
	No. of tests in which spiders interacted	30	10	24	20
Web present	No. of tests	55	50	46	56
	No. of tests in which intruder touched web	40	36	39	45
	No. of tests in which spiders touched each other	26	18	14	10
	No. of tests in which spiders interacted	33	27	24	25

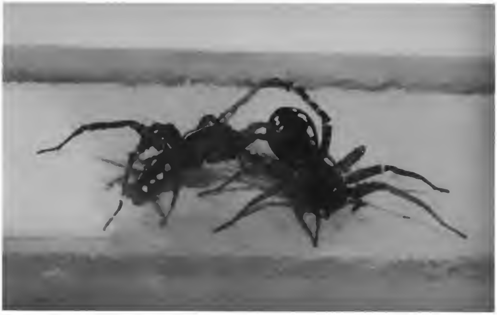


Fig. 18 *Supunna picta* male (left) drums on female (right, side-on to male). Female raises her abdomen and right leg IV.

Besides using tactile and vibratory displays, clubionids probably make extensive use of pheromonal communication. Peck & Whitcomb (1970) suggested that *Chiracanthium inclusum* males initiate courtship when they detect female pheromones, and Pollard & Jackson (1982) gave experimental evidence that *Clubiona cambridgei* uses nest-associated sex pheromones. *S. picta* males performed courtship displays after contacting webs and draglines of females, suggesting that silk-associated pheromones are important in this species, too.

COHABITATION AND MALE-SUBADULT INTERACTIONS

It was common to find males sharing webs with subadult females in nature. We collected three such cohabiting pairs and each subadult matured within 1 week.

Male-subadult interactions (Table 4) in the laboratory were usually brief and similar to brief male-female interactions, but five tests with webs present led to cohabitation. Each of these five subadults was 3–6 days from maturity, whereas subadults were 10–26 days from maturity in all other tests with webs present. Each of these five males drummed and laid down silk, entered the web, then became quiescent. Each of these pairs remained together until the females moulted, after which these females were kept isolated from other *S. picta*; 30–50 days later, they oviposited fertile eggs, indicating that they had mated.

Table 5 Reults of male-female interactions.

		Virgin female	Previously mated female
No web present	Interactions	12	18
	Mated	67%	0
Web present	Interactions	11	22
	Mated	100%	0

Cohabitation of males with subadult females is a widespread mating tactic of both web building and cursorial spiders. Jackson (1986a) provided records for 161 species, including 13 clubionids (6 species of *Chiracanthium* and 7 species of *Clubiona*). The male of each of these 13 clubionid species builds, and stays in, a separate chamber fastened to the female's nest. *S. picta* differs because the cohabiting male and subadult female of this species share a common web.

Pollard & Jackson's (1982) arguments about the adaptive significance of cohabitation in *Clubiona cambridgei* probably apply also to *S. picta*. In both these spiders, virgin females mated readily, but previously mated females did not remate. Because the unwillingness of females to remate makes receptive females a limiting resource for males, it may be highly advantageous for a male to stay with a subadult female until she matures.

What advantages do subadult females gain by allowing males to cohabit? Female *S. picta* can lay several egg sacs after a single mating, and cohabitation assures the female a supply of sperm from the start of her adult life, which may be important in maximising the number of fertile eggs she can produce during her lifetime. On the other hand, perhaps subadult females cannot displace males from webs. The subadult might end cohabitation by decamping, of course, but the cost (loss of nest) of getting rid of the male this way may be too great.

PHYLOGENETIC CONSIDERATIONS

Although this is the first report of web building by a clubionid, web-building species are known from some other families traditionally regarded as cursorial hunters: the Lycosidae (e.g., Brach 1976), Gnaphosidae (Jarman & Jackson 1986), Oxyopidae (Griswold 1983), Pisauridae (e.g., Nentwig 1985), Salticidae (Jackson 1986c), and Thomisidae (S.D. Pollard, pers. comm.). Each of these families may have evolved from web-building ancestors and, in fact, all araneomorph spiders may have had web-building ancestors (Coddington 1986; Jackson 1986c; Shear 1986;). Some of the web-building species in these families practise a type of predatory versatility in which each individual of a species is both a cursorial and a web-building spider. It is tempting to envisage species with predatory versatility as being in, more or less, a transitional stage of spider evolution; they would appear to have adopted cursorial predation without fully giving up web building.

Perhaps *S. picta* is such a "transitional" species, but ascertaining the relevance of this species biology to clubionid evolution is problematical because, as currently constituted, Clubionidae is probably polyphyletic (see Lehtinen 1967). The relevance of *S. picta's* biology for understanding the evolution of better known clubionids, such as *Clubiona* and *Chiracanthium*, will have to be reconsidered when, and if, this family is revised.

Supunna picta's predatory behaviour is markedly different from that usually associated with clubionids, but its reproductive behaviour resembles what little is known about other clubionids. Most differences are probably related to *S. picta* not having dense nests: *S. picta* males and subadult females cohabit within a web rather than side-by-side in separate nest chambers; during courtship and mating, *S. picta* males do not use (or need to use) behaviours to by-pass the physical barrier of a nest; the copulatory posture of *S. picta* resembles that of most hunting spiders, but differs from the aberrant position of *Chiracanthium inclusum*. The egg sac of *S. picta* is atypical for a clubionid but closely resembles egg sacs of other species from the clubionid subfamily Castianeirinae (unpubl. data), the subfamily to which *S. picta* probably belongs (Reiskind, pers. comm.). Possibly, castianeines have evolved independently of most other spiders now in the family Clubionidae and the castianeines, at least, may have had a strictly web-building ancestor.

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Mechanisms for turn alternation in the tunnelling mud crab *Helice crassa*

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Abstract Turn alternation, or the tendency to turn in the opposite direction to a preceding forced turn, was investigated experimentally in tunnelling mud crabs near their natural habitat. Although crabs alternated significantly following a forced turn of 45°, 90°, or 135°, there were no significant differences between these conditions. When required to negotiate sequentially three 90° forced turns in one direction followed by a fourth in the opposite direction, the crabs subsequently alternated the last turn, thereby turning in the same direction as the earlier three. The results of the two experiments confirmed a suggestion that, unlike many other invertebrates, mud crabs alternate tactile rather than proprioceptive stimuli when in experiments faced with vertical surfaces. In such situations their thigmotactic behaviour appears to dominate any influence of response-generated proprioceptive cues.

Keywords Tunnelling mud crab; *Helice crassa*; turn alternation; thigmotaxis; proprioception

INTRODUCTION

The tendency to turn in the opposite direction to a preceding turn has been described in laboratory settings for a number of invertebrate species ranging from flatworms to insects (Hughes 1989a). It has been suggested that this tendency gives rise to patterns of alternating turns which, in the absence of directional cues, correct for deviations from linear paths of movement (Barnwell 1965; Hughes 1967). In the natural environment these patterns would accordingly facilitate exploration, dispersal, foraging, and escape behaviour.

In most instances the specific mechanism underlying turn alternation appears to involve storage of mainly proprioceptive information about previous turns which might arise from the distortion of body segments (Schäfer 1975, 1982) or, at least in isopods, from bilaterally-asymmetrical leg movements (Hughes 1985, 1989b,c). Although, for most species, crucial involvement of tactile cues alone now seems unlikely (Schäfer 1972, 1975; Hughes 1989a), an ungraded thigmotactic tendency could be important under certain circumstances. It appears that while alternating, (1) different species may vary in the use of tactile relative to proprioceptive cues, and (2) species for which proprioceptive cues are normally important may behave thigmotactically in the presence of excessively strong tactile stimulation (Hughes 1987).

Since terrestrial isopods are the only crustaceans for which turn alternation rather than repetition has been described, further evidence for alternation was sought by investigating its existence (or otherwise) in a decapod representative. In an earlier study (MacKay 1945), the hermit crab *Calcinus herbsteii* was shown during several consecutive trials to repeat its turns by always choosing the arm of a T-maze on the same side as its larger left cheliped.

The species chosen for the present study was the New Zealand tunnelling crab, *Helice crassa*, because of its abundance, convenient small size, tendency to move quickly in a straight line, and ability to live out of water for long periods of time (McLay 1988). This

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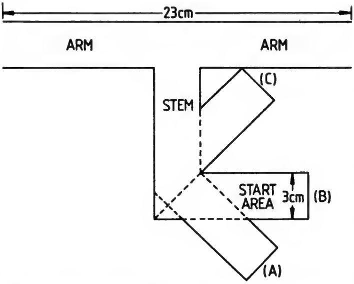

Fig. 1 T-maze(s) (drawn to scale) with a forced right turn of (A) 45°, (B) 90°, or (C) 135°. Left forced turns were provided by inverting the example(s) shown.

species inhabits sheltered estuarine areas in all parts of New Zealand (McLay 1988). It tolerates a wide range of salinities and temperatures and is exposed to air for 5–9 h during each tidal cycle.

H. crassa digs and lives in a burrow which it defends against intruding crabs, retreats to when disturbed, and from which it emerges to feed at low tide (McLay 1988). Therefore, in addition to correcting for deviations while outside, a tendency towards alternating turns would assist *H. crassa* in maintaining a linear path of movement during construction of its sloping but straight burrow. Linear burrow construction and movement would be assisted by the bilateral symmetry in size of chelipeds and walking legs that characterise this species (McLay 1988).

EXPERIMENT I

In species for which turn alternation depends primarily on proprioceptive information about earlier movement sequences, there is an increasing probability of alternating with sharper preceding turns (see Hughes 1989a for a summary). This first experiment was designed to determine if *H. crassa* would alternate when allowed a left or right free turn following a forced turn of varying size in either direction.

Methods

At afternoon low tide during 9–17 January 1989, crabs were dug from burrows in mudflats of the Opara river estuary, Okains Bay, Banks Peninsula, Canterbury, New Zealand. They were tested immediately and then returned to the general vicinity of their individual habitats.

The experimental apparatus comprised three galvanised steel floorless T-mazes with open-ended arms and stems bent to produce a forced-turn angle of 45°, 90°, or 135° to the left or right (Fig. 1). Each 3 cm high maze sat on level damp sand with the T-junction facing towards the sun, ensuring that light and shade were evenly balanced for each arm.

Crabs with a carapace width of 1.5–2.0 cm were lowered individually into the start area of a maze and allowed to negotiate the forced turn, move into one of the arms, and then escape. Thirty crabs were observed in each maze with half of each group being forced left and half forced right.

Results

The number turning in the opposite direction to the forced turn is shown in Table 1. There was no significant difference in alternation between those forced left and those forced right ($\chi^2 = 0.9$, d.f. = 1, N.S.) nor were there any differences between effects of the three forced-turn angles ($\chi^2 = 0.42$, d.f. = 2, N.S.). However, in each forced-turn condition the number of crabs that alternated was significantly greater than chance: 45° and 90°, $z = 2.74$, $P = 0.006$ in both instances; 135°, $z = 3.10$, $P = 0.002$.

Discussion

The lack of any relationship between forced-turn angle and free-turn behaviour suggests that the crabs used tactile rather than proprioceptive cues in their turn alternation. There was no evidence of a quantitative relationship between amount of tactile stimulation and size of a subsequent turn, found when proprioceptive mechanisms are involved (Hughes 1989c; Schäfer 1972). That crabs used tactile cues was supported by general observations of their behaviour in the maze: before reaching a forced turn, each crab crawled sideways along the stem with its posterior margin in contact with a wall. If it had been following the wall on the outer side of the turn it continued following this wall while turning and then later entered the nearest arm, namely that requiring a turn opposite to the forced turn. On the other hand, if it had been following the inner wall it also continued to follow this wall around the forced turn but, in most instances, was carried forward to some extent by its own momentum. This so-called "centrifugal swing" (Schneirla 1929) accordingly brought it into contact with the outer wall of the post-turn stem which it then appeared to follow at the T-junction, thereby alternating with respect to the forced turn. Those few crabs that failed to alternate were all slow-moving inner wall-followers for which centrifugal swing did not operate at the forced turn. Consequently they continued following the inner wall and on reaching the T-junction inevitably turned in the same direction as the forced turn.

EXPERIMENT II

Even though thigmotactic responses are important in decapod orientation behaviour (Pardi & Papi 1961), the wall-following that presumably determined *H. crassa's* turn alternation in Experiment I might still have been caused by a proprioception-mediated mechanism. Research with isopods has shown how such a mechanism can still lead to apparent wall-following and then alternation after negotiation of a forced turn (Hughes 1985, 1989b). However, if an animal experiences several 90° forced turns in one direction followed by a single turn in the opposite direction and then a free choice, it is possible to distinguish between the predominant role, when alternating, of proprioceptive and tactile cues. The cumulative effects of response-generated proprioceptive stimuli arising from several unidirectional turns are unlikely to be entirely dissipated by the effect of a single turn in the opposite direction (Hughes 1985, 1987). Therefore, if proprioception is dominant, animals experiencing this situation should repeat the last turn thereby alternating with respect to the preceding turns. This outcome should also occur if the ineffectiveness of different forced-turn angles observed in Experiment I had been merely because of a ceiling effect arising from uniformly high levels of alternation in all conditions. But, if a thigmotactic tendency is primarily responsible, at the final turn, centrifugal swing should take the animal away from the wall it had been following and bring it into contact with the opposite wall. Then by following this new wall it should alternate with respect to the final forced turn, thereby turning in the same direction as the preceding turns.

Methods

Further crabs were collected from the same location and treated in the same general manner as those observed in Experiment I. They were each allowed to make either a left or right turn at a T-junction after having negotiated three consecutive 90° right turns followed by a 90° left turn (12 crabs) or three left turns followed by a right turn (12 crabs). The 3 cm high galvanised steel floorless apparatus is described in Fig. 2 along with free-turn pathways predicted from interpretations based on the use of proprioceptive and tactile cues.

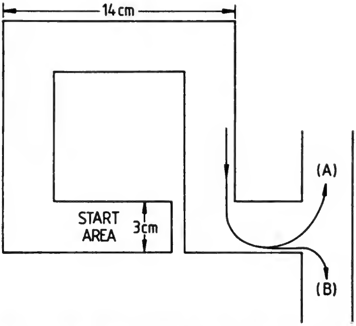

Fig. 2 Maze (drawn to scale) involving three 90° forced right turns followed by one to the left, and predicted direction of free turning according to the use of (A) proprioceptive or (B) tactile cues. Forced turns in the opposite directions were provided by inverting the maze.

Results

At the T-junction only one of the 12 crabs forced right three times and then left once, and two of the 12 that experienced the opposite sequence, failed to alternate with respect to the fourth forced turn. The total number of alternators (21) significantly exceeded chance ($P < 0.002$).

Discussion

These results were consistent with tactile rather than proprioceptive cues being primarily responsible for the crabs' turn alternation (prediction B, Fig. 2). Since they turned in the same direction as the first three turns, their choices were determined by the vertical surface they were in contact with immediately before reaching the T-junction. Consequently, indications of apparent thigmotaxis-based wall-following behaviour in Experiment I were confirmed.

GENERAL DISCUSSION

By responding to tactile rather than proprioceptive cues, *H. crassa* joins a minority of invertebrate species for which a combination of centrifugal swing and thigmotaxis may be primarily responsible for turn alternation, e.g., *Lumbricus rubellus*, *Ophiulus pilosus* (Hughes 1987). Although decapods do not utilise as many cues in their orientation behaviour as other crustaceans such as amphipods (Rebach 1983), according to the principle of redundancy it is unlikely that their turn alternation would always depend on tactile cues alone. In situations where tactile stimulation from vertical surfaces is minimal or absent, it is clear that *H. crassa* is able to successfully orient itself, feed, mate, and engage in agonistic behaviour (McLay 1988) through the use of proprioceptive as well as other cues. Nevertheless, as with certain other species (Hughes 1987), it is possible that, when alternating, a thigmotactic tendency could dominate proprioceptive influences if tactile stimulation exceeds a minimal level. Hence the behaviour would reflect interactions between an idiothetic tendency to maintain linear movement and an allothetic tendency to orient towards tactile stimuli. These interactions have been described for myriapods and insects in response to light and gravitational stimuli (Mittelstaedt-Burger 1972; Mittelstaedt et al. 1979). A shift from mainly idiothetic control might suggest that when threatened, orientation towards tactile stimulation provides a more efficient means of escape. While collecting experimental animals, it was noted on several occasions that, when encountering an object such as a rock or mollusc shell, a fleeing crab immediately assumed close contact with the object, and walked around it; at the same time, it appeared to seek a means of crawling under it. There were also apparent attempts to dig under walls of mazes when corners were encountered at forced turns. Alternatively, a thigmotaxis-based allothetic tendency might only operate for short distances, since idiothetic orientation controls the location of burrows over longer distances in other crabs such as fiddlers (Herrnkind 1983).

Whether or not *H. crassa* will alternate proprioceptive or other stimuli in the absence of significant tactile stimulation could be determined by adopting techniques which eliminate the need for vertical surfaces, e.g., elevated runways without walls. Because a threat might encourage thigmotactic rather than other forms of behaviour, it could also be desirable to devise experimental procedures which minimise the presumably stressful elements characterising those used in the present study. Nevertheless, when experiencing the standard procedures, *H. crassa* differs from most other invertebrates so far investigated by relying on tactile rather than proprioceptive cues for turn alternation.

Table 1 Numbers of crabs that alternated following a forced left or right turn of 45, 90, or 135°.

Direction of forced turn	Forced-turn angle (in degrees) 45	90	135
Left ($n = 15$)	12	12	12
Right ($n = 15$)	10	10	11
Total (%)	22 (73)	22 (73)	23 (77)

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New Zealand distribution and seasonal incidence of the nematode, *Sphaerularia bombi* Dufour, a parasite of bumble bees

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Abstract In New Zealand the nematode *Sphaerularia bombi* Dufour is currently confined to an area of about 30–40 km around Christchurch, where bumble bees were originally released. The spread of this nematode has been much slower than that of its bumble bee hosts during the 100 years since their introduction. Levels of apparent parasitism of up to 56% in *B. terrestris* (L.) and 7% in *B. hortorum* (L.) were detected. The incidence of *S. bombi* queens foraging in spring rises sharply as healthy queens become unavailable when they start their nests. Estimated mortality levels caused by *S. bombi* are between 3–10% in both *B. terrestris* and *B. hortorum*. These levels are lower than in Europe. Infected *B. terrestris* averaged 5.0 nematode uteri per host and *B. hortorum* 1.7 uteri per host, which is similar to records from Europe. The status of *S. bombi* as a parasite of *Vespula* queens remains uncertain.

Keywords *Sphaerularia bombi*; distribution; seasonal incidence; *Bombus*; mortality

INTRODUCTION

From 1883 until 1885, 1490 bumble bee queens of at least three species were imported from England and sent to Canterbury and Waikato in New Zealand (Anon. 1884; Farr 1889; Hopkins 1916; Gurr 1964); Pareora received 18 queens, Christchurch 806 queens, and Matamata over 645 queens. At best only 25% of these queens survived the 8–9 week journey, and nearly all the queens died in the 1883 and 1884 shipments. In 1883 two live queens were released near Pareora, Canterbury and two at Matamata in the Waikato in 1884. There was no establishment at Matamata and apparently none near Pareora. In 1885 releases at two sites in Christchurch (Fig. 1) resulted in the establishment of *B. terrestris* (L.), *B. ruderatus* (Fabr.), and perhaps *B. subterraneus* (L.). Queens descended from these populations reached Pareora by 1887, which would have masked any earlier establishment. In 1906, the Canterbury Acclimatisation Society imported three more species, including *B. hortorum*. A total of 180 queens were taken to Lincoln College and 145 to Tai Tapu (*Christchurch Press* 1906; Lamb 1964). In 1970, the nematode *Sphaerularia bombi* Dufour was found in bumble bee queens from Christchurch and around Lincoln in Canterbury (Macfarlane 1975).

The primary aim of our survey was to determine where *S. bombi* had established and how far it had spread. There was a need to determine if areas free of this nematode existed, because by 1965, queens had begun to be shifted around New Zealand (Gurr 1972). Also, collection and release of queens onto farmers crops had been proposed to improve pollination (Clifford 1973). Attempts were made to establish *B. ruderatus* in the Chatham Islands in 1976 (Macfarlane 1980) and *B. hortorum* in Marlborough in 1979 and 1980 Marlborough (Macfarlane & Griffin unpubl. data) by collecting queens in Marlborough and South Canterbury, respectively. Secondary aims of our study were to determine how the changes in *S. bombi* incidence were related to seasonal activity of bumble bees in New Zealand and to discover if levels of parasitism were comparable to those of the same hosts in Europe.

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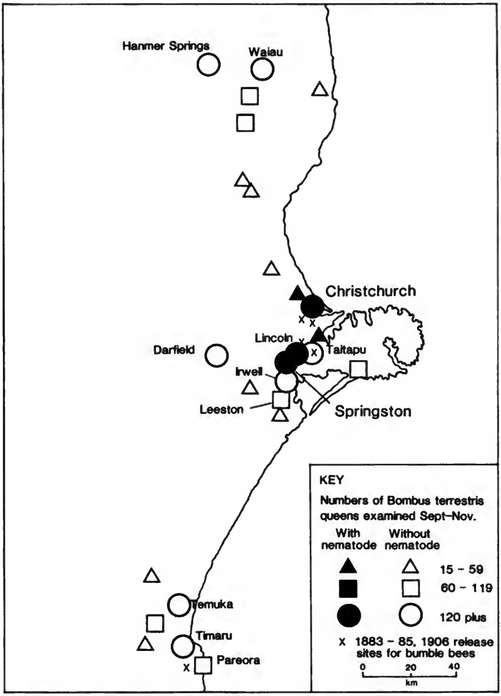

Fig. 1 Localities in Canterbury sampled for *Sphaerularia bombi* 1970–1977.

Sphaerularia bombi has free-living stages in the soil followed by parasitic stages (Poinar & van der Laan 1972). This nematode is very unusual, because of the greatly enlarged uterus it develops in the queen's abdomen and its ability to sterilise its host by keeping the corpora allata small and inactive. Consequently, infected queens cannot start colonies, and so workers and males are not affected (Postner 1951; Alford 1968; Poinar & van der Laan 1972; Macfarlane 1974; Pouvreau 1974). In late summer and autumn, mated female nematodes are picked up as the queens hibernate in the soil. By spring a full-sized nematode uterus has developed within the queen's haemocoel when she emerges from hibernation. More than 100 000 nematode eggs can be released within the queen's haemocoel where they hatch. Third instar larvae penetrate the gut, where they are gradually voided in the faeces. In late spring, queens infected by *S. bombi* dig into the topsoil at sites that overlap with hibernation sites (Poinar & van der Laan 1972; Macfarlane 1974; Lundberg & Svensson 1975) and more nematode larvae are voided at this stage. Infected queens eventually die with some nematode larvae, probably resulting in aggregations of *S. bombi* in the soil, judging by variations in the number of *S. bombi* infecting queens. Nematodes released to the soil moult twice and mate.

Sphaerularia bombi has been recorded from 22 European and 15 American species of Bombinae (Macfarlane 1973, 1974; Lundberg & Svensson 1975). Hosts have yet to be checked for it in Asia and Central and Southern America. *Vespula rufa* L. and the common wasp *V. vulgaris* L. are recorded as hosts (Schneider 1866; Stammer 1934). However, Pouvreau (1963) could not verify this and Spradbery (1973) and Edwards (1980) do not recognise *S. bombi* as a wasp parasite.

In Europe a considerable and rapid increase in the apparent level of *S. bombi* parasitism of *B. terrestris* occurs during spring and summer (Fig. 2). Thus, the timing of any survey has a crucial effect on the results. Generally, species of *Bombus* that emerge earlier in the season, e.g., *B. terrestris*, have higher overall levels of parasitism (Macfarlane 1973, 1974) than later-emerging species such as *B. hortorum* and *B. subterraneus* (Donovan & Macfarlane 1984; Prys-Jones & Corbet 1987). The overall level of parasitism of 658 *B. terrestris* queens collected between March and July in Europe was 35.4% (Lubbock 1861, 1864; Palm 1945; Cumber 1949; Hattigen 1956; Hasselrot 1960; Pouvreau 1962, 1964; Alford 1969; Stein & Lohmar 1972).

By contrast, 111 *B. hortorum* queens averaged only 17%parasitism (range 0–67%) with no conclusive seasonal pattern (Lubbock 1861; Palm 1945; Cumber 1949; Hasselrot 1960; Alford 1969; Stein & Lohmar 1972). Two of the 10 *B. subterraneus* examined had *S. bombi* (Lubbock 1861; Hasselrot 1960). There are no studies of *S. bombi* in regions where hosts continue to fly throughout the year. Such extended activity occurs in much of coastal New Zealand and some southern parts of the Northern Hemisphere.

METHODS

This survey for *S. bombi* examined overwintered queens of 3780 bumble bees from Canterbury (Tables 1–2, Fig. 1) and 153 from the Waikato, mainly in the vicinity of the six release sites of live bumble bees. The collection sites were on flat land except for some of the queens from Hanmer Springs, Timaru, and near Christchurch. One hundred and nine overwintered queens were also collected from Marlborough and Central Otago (Table 2). Collection of these queens was made between 1969 and 1977, and was concentrated in mid spring (Table 1) when queens and nematodes should be commonest. Most bumble bee queens were taken from flowers. Also, a few queens searching for nests or that were founding nests, i.e., with pollen on their hind legs, were collected. Between December 1969 and March 1971, 138 new queens were collected from flowers, of which 47 were from Christchurch and Lincoln, and 91 from Tai Tapu to Southbridge. Between 1974–1977, 21 queens of German wasps *Vespula germanica* (Fabr.) were collected from the same flowers as the bumble bees. Of these, 10 were from Christchurch, Belfast, and Lincoln.

Queens were weighed, their abdomens dissected, and the number of nematode uteri was recorded. From 1975 onwards the presence and proportion of nematode eggs and larvae was also noted.

RESULTS

The extensive survey of Canterbury revealed that *S. bombi* occurs in Belfast, Christchurch, Lansdowne Valley, Governors Bay, Prebbleton, Lincoln, and Springston (Table 1). Tests on 10 or more *B. terrestris* in October or November revealed *S. bombi* in all the five flat sites in Christchurch. *S. bombi* was found on Cashmere Hills, but not on four other nearby hill sites on Banks Peninsula. All other locations sampled in Canterbury, Central Otago, Marlborough, and Waikato were free of this nematode (Fig. 1, Table 2).

Sphaerularia bombi was found in 67 of 978 overwintered queens of *B. terrestris* and 3 of 148 *B. hortorum* queens in the vicinity of Christchurch and Lincoln (Table 1). *S. bombi* was not detected from either *B. hortorum* or *B. ruderatus* in the Lincoln/Springston area, nor was it found in new queens. No nematodes were found in the German wasp queens.

In September, most *S. bombi* had begun or just completed releasing eggs from the uterus into the *B. terrestris* queen's haemocoel. As spring proceeded, *S. bombi* larvae were the main developmental stage in an increasing proportion of queens (Table 3). Queens with *S. bombi* uteri only were found as late as 31 October and at Springston with only eggs and uteri on 15 November. Two infected *B. terrestris* queens died on 17 and 26 November after being confined in rearing boxes for 7 and 11 days. By mid October, in contrast, most healthy queens remain in the nest they have started and they can survive until December/January (Macfarlane & Griffin unpubl. data). The basal level of parasitism in nectar-foraging queens of *B. terrestris*, was 3–6% in early spring, i.e., within 1 month after most queens emerge. The apparent incidence increased about 10-fold during the second half of October and November (Fig. 3). This increase occurred 3–4 weeks earlier in Christchurch than in the Lincoln/Springston area.

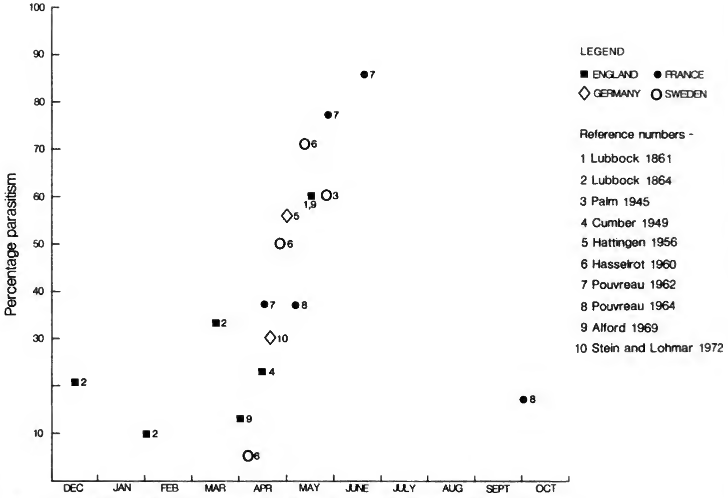

Fig. 2 Levels of *Sphaerularia bombi* observed in *Bombus terrestris* queens from Europe.

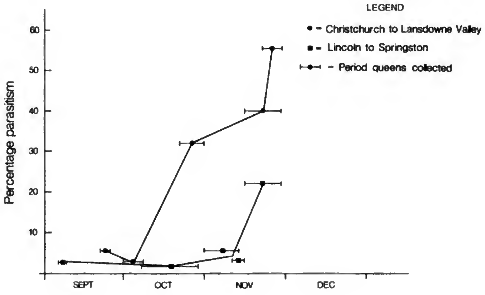

Fig. 3 Change in *Sphaerularia bombi* levels in overwintered *Bombus terrestris* queens in Canterbury, New Zealand.

Fifty-five infected queens of *B. terrestris* averaged 827 ± 87 mg in weight, which was 17% heavier than 1150 healthy queens that averaged 706 ± 3 mg.

The infected *B. terrestris* queens had a mean of 5.0 ± 0.8 uteri per host (range 1–32; *n*=67). The length of uteri in the most heavily infected hosts were 70% of those in hosts with the fewest uteri (Table 3). The infected *B. hortorum* queens averaged 1.7 uteri (range 1–2) per host. No nematode eggs were observed in queens caught from 6 October to 16 November.

DISCUSSION AND CONCLUSIONS

In 1883–1885, most of the bumble bee queens were collected from England in November and December, so virtually all must have been overwintering in the soil. At this stage of the season, incidence of *S. bombi* seems relatively low (Fig. 2). So many queens were shipped to New Zealand that some must have had *S. bombi* in them. Somehow, the soil near the 1885 release site was contaminated, as the current distribution of *S. bombi* closely matches the sites of establishment of bumble bees near Christchurch. The probable lack of live hosts for 3–5 years in South Canterbury and their certain absence from Waikato could account for the failure of *S. bombi*, to establish there. If the two live bumble bees imported to South Canterbury established a population then they must have been free of *S. bombi* because our survey should have detected any *S. bombi* there. Subsequent importations of bumble bees to Canterbury in 1906 may have provided a supplementary source of *S. bombi*. However, fewer queens were imported and they included species that are less heavily affected by *S. bombi*. *Vespula* wasps, which are the only possible alternative hosts, are not implicated in the establishment of *S. bombi* in Canterbury, because the later accidental introductions were all in the North Island (Thomas 1960; Donovan 1984).

It is not clear if *B. ruderatus* and *V. germanica* are *S. bombi* hosts in New Zealand as only a few queens were collected from sites where *S. bombi* occurs. If this nematode affects these species, then the greatest incidence of *S. bombi* should occur in November and December. This prediction is based on the seasonal incidence of *S. bombi* in *B. terrestris* and comparative studies on nest establishment of bumble bees and German wasps in coastal Canterbury (Macfarlane & Griffin unpubl. data).

S. bombi sterilises all queens in autumn and winter, so in a life table it acts as a mortality factor before colony initiation, even although the actual

Table 1 Number of bumble bee, *Bombus*, and wasp, *Vespula*, queens examined in central Canterbury and the incidence of parasitism by the nematode *Sphaerularia bombi* (in brackets).

Locality	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Total
					B. terrestris							
Christchurch-Belfast	0	0	0	0	55(3)	152(40)	28(14)	2	10	0	4	251
Halswell-Lansdowne Valley	0	26	48	0	1	56	5(1)	0	14	0	4	154
Avoca Valley, Sumner, Governors Bay	0	0	0	0	0	67	0	0	0	0	0	67
Prebbleton, Lincoln	2	47	28	102	39(1)	80(1)	115(7)	2	6	2	0	423
Springston	0	0	0	0	0	88	39(1)	0	0	0	0	127
Total	2	73	76	102	95	443	187	4	30	2	8	**1022**
Average % parasitism	0	0	0	0	4.2	9.3	12.3	0	0	0	0	–

	Jun	Jul	Sep	Oct	Nov	Jan	Total	Oct	Nov	Total	Oct	Nov
				B. hortorum				***B. ruderatus***			***V. germanica***	
Christchurch-Belfast	0	0	4	29(1)	30(1)	2	65	3	2	5	1	8
Governors Bay	0	0	0	14(1)	0	0	14	2	0	2	0	0
Lincoln	1	1	0	12	40	1	55	19	43	62	1	0
Springston	0	0	0	3	14	0	17	24	24	48	0	0
Total	1	1	4	58	84	3	**151**	48	69	**117**	2	8
Average % parasitism	0	0	0	3.4	1.2	0	–	0	0	–	0	0

Table 2 Number of overwintered *Bombus* queens examined in the vicinity and beyond the original bumble bee release sites.

	Number of *Bombus* queens		
Locality	*terrestris*	*hortorum*	*ruderatus*
Tai Tapu, Greenpark	135	23	47
McQueens Valley – Birdlings Flat	108	0	3
Irwell–Coes Ford	178	1	14
Leeston, Southbridge	73	5	80
Dunsandel	21	1	0
Darfield, Hororata, Sheffield	214	16	265
Rangiora, Kaiapoi,	25	1	6
Total Mid Canterbury[1]	**754**	**46**	**175**
Geraldine	25	7	0
Temuka, Winchester	145	5	3
Pleasant Point	95	2	1
Near Cave	32	0	0
Timaru	123	2	0
Pareora, St Andrews	202	0	0
Total South Canterbury[2]	**622**	**16**	**4**
Matamata:Waikato	118	–	5
Tirau, Tokoroa:Waikato	30	–	0
Kaikoura–Picton:Marlborough	41	–	46
Conway Flats–Waipara: North Canterbury	829	–	40
Arthurs Pass–Mackenzie Basin: Inland Canterbury*	31	1	4
Lindis Pass – Clyde: Central Otago	16	0	6

– = Not present in this area * 3 *B. subterraneus* queens examined too.
1 = Locations within 40 km of the area known to have *Sphaerularia bombi*
2 = Locations within 40 km of the other bumble bee release sites.

Table 3 Development stages and uterus lengths of *Sphaerularia bombi* in *Bombus terrestris*.

	Percentage of hosts at each development stage of *S. bombi*			
Number of *B. terrestris* examined	Uteri only or a few eggs	Mainly eggs few larvae	Mainly larvae	Months
3	33	33	33	September
40	5	30	65	October
18	0	17	83	November
Number of uteri per host	Uterus length (mm) of *S. bombi* Average SEM	Range		
1–2	24.0 ± 0.7	14.0–36.0		
3–5	20.8 ± 0.5	10.0–29.0		
6–10	20.6 ± 0.6	9.0–34.0		
11–31	16.6 ± 0.3	6.0–26.0		

death of infected queens occurs later when colonies with healthy queens are growing. Estimating mortality levels caused by *S. bombi*, before nest initiation is difficult. Ideally, queens should be taken directly from hibernation sites upon emergence or from hibernaculae in early spring. This is not yet practical as current methods of locating these queens are slow, even though the general habitat of the hibernacula of various species, including *B. terrestris* and *B. hortorum*, is known (Macfarlane 1974; Alford 1975). The marked increase in apparent parasitism in *B. terrestris* is correlated with nest initiation by healthy queens, which stop foraging soon after their first workers emerge (Donovan & Macfarlane 1984). Consequently, late spring and early summer samples from flowers seriously overestimate the impact of *S. bombi* on bumble bee populations. Even the lower percentage of parasitism in early spring is at best an approximation, because the parasitised and heavier queens (Macfarlane 1974, this study) could emerge later in the season than normal queens. Certainly lightweight (Holm 1972) and diseased queens (Macfarlane 1974, 1976) emerge earlier and soon die.

Considering all the factors, we estimate that *S. bombi* causes 3–10% mortality of both *B. terrestris* and *B. hortorum* in Canterbury. Mortality seems to be lower on the fringe of the region with *S. bombi*. Here the soils or sites are drier in summer when the nematodes are released from the host; warm and wetter seasons or locations apparently favour nematode survival and reinfection of hosts (Pouvreau 1963; Alford 1969). Both the upper and lower levels of parasitism of *B. terrestris* by *S. bombi* are lower in New Zealand than Europe. However, the number of uteri per infected host is similar to English and French records (Pouvreau 1964; Alford 1969) and the number of uteri per infected host is generally linked to different parasitism levels in hosts by *S. bombi* (Alford 1969; Macfarlane 1974). These relative indices of parasitism provide conflicting evidence on the impact of *S. bombi* in these regions.

Some healthy *B. terrestris* queens spread up to 140 km a year during their establishment (Hopkins 1914) and have colonised at least 23 islands 2–30 km offshore (Macfarlane unpubl. data). However, *S. bombi* is restricted to within 30–40 km of the four release sites of 1884–1885 and 1906, which gives a calculated dispersion rate of less than 0.5 km per year. The long dispersal flights of new queens in autumn (Mikkola 1978) does not involve *S. bombi*, because new queens are not yet infected. In spring, healthy queens disperse gradually but continually as they search for nest sites in spring (Wyatt 1970), but queens with *S. bombi* do not search for nests, because the corpora allata and ovaries never develop properly (Poinar & van der Laan 1972). This probably explains why infected queens tend to stay with satisfactory food sources once they have found them and do not disperse widely, even although many such queens continue flying later in the season than healthy queens, which cease foraging soon after their colony becomes established. Demonstration of the effect of the nematode on queen dispersal is unique, because Canterbury is the only place where bumble bees with *S. bombi* were imported and established in an area previously devoid of bumble bees.

As the distribution of *S. bombi* in New Zealand is known, domestication of bumble bees can begin without the handicap of losses of queens caused by *S. bombi* that are experienced in Europe and North America. Nematode-free queens of bumble bees from the field have been exported by the authors to Europe and North America for trials on breeding bumble bees. New Zealand was chosen as a source of long-tongued bumble bees for Chile, partly because queens without any *S. bombi* could be collected directly from the field (Arretz & Macfarlane 1986).

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Seasonal, geographical, and age-related variations in the diet of the yellow-eyed penguin (*Megadyptes antipodes*)

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Abstract A quantitative study of yellow-eyed penguin diet was carried out at two mainland breeding areas over a 2-year period, and at five other breeding areas over shorter time periods. Yellow-eyed penguins (*Megadyptes antipodes*) ate 26 prey species, with fish comprising 87% of the weight and 91% of the total number of prey items. Sprat occurred in the largest number of stomachs (70%) with red cod, opalfish, and squid in 49%, 42%, and 46%, respectively. Most prey items were <200 mm long. Prey were mainly pelagic species but also demersal species. The absence of inshore species in the diet and the distributions of prey species indicated that penguins travel away from the coast before beginning to feed, but remain over the continental shelf. Juvenile penguins ate more squid and less fish than adults, and weighed less. Differences in diet composition, body weights, and meal sizes were found between birds from different breeding areas, and between breeding seasons of contrasting reproductive success. Evidence from preferred prey and daily foraging patterns suggested that yellow-eyed penguins are selective feeders, and as such, are vulnerable to fluctuations in populations of their preferred prey.

Keywords diet; prey; penguin; yellow-eyed penguin; *Megadyptes antipodes*

INTRODUCTION

Yellow-eyed penguins (*Megadyptes antipodes*) are present throughout the year at their breeding areas which are scattered along the south-east coast of New Zealand's South Island, Stewart Island, the Auckland Islands, and Campbell Island. During most of the year penguins leave the breeding area at dawn to feed and return at dusk, although this pattern may become less regular when feeding chicks (Richdale 1957). The total population is estimated at 7000 individuals, with only 600–700 pairs breeding on mainland New Zealand (J. T. Darby pers. comm.).

Recent censuses indicate that numbers have decreased since counts were last made (1936–1954) (L. E. Richdale 1942, unpublished manuscript, Hocken Library, Dunedin, New Zealand; 1957; J. T. Darby pers.comm.). Poor reproductive success seems to be because of destruction of nesting habitat and increasing predation (Darby 1985). In some seasons, starvation of chicks and adults, and low fledging weights result in mortality, and hence poor recruitment into the breeding population (van Heezik & Davis 1990). The frequency of such poor seasons may be increasing; Richdale (1957) recorded only one season with mortality resulting from starvation in 18 years, whereas starvation occurred in three years between 1983 and 1988 (van Heezik 1988).

Knowledge of diet is necessary to determine the extent to which yellow-eyed penguins depend on particular prey. The aims of this study were to outline diet composition, to describe diet in terms of prey size and variety of prey items, and to compare the diets of adults and juveniles. As variations in reproductive success were found between breeding areas (van Heezik 1988), diet was studied at several breeding areas to determine whether its composition was the same, and if not, whether differences in composition might explain variations in reproductive

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success. Diet was also compared between two seasons to help determine whether diet composition was related to reproductive success.

METHODS

The study animal. The yellow-eyed penguin breeds on the south-eastern coast of the South Island, New Zealand, and on Stewart, Auckland, and Campbell Islands (Falla et al. 1981). Usually two eggs are laid between late September and early October, followed by an incubation period of about 43 days (Richdale 1957). Eggs hatch in the first 3 weeks of November. During the first 6 weeks chicks are guarded by one or other of the parents, after which both parents forage each day and return to feed chicks in the afternoon or evening. Total fledging period is about 105 days, and chicks are fed right up until their departure, although frequency of feeding may taper off (Richdale 1957).

Sampling regime. The main study was carried out at two breeding areas: Nugget Point (46°20′S, 169°40′E), from March 1984 to June 1986, and Boulder Beach (45°50′S, 170°30′E), from July 1984 to August 1986. Stomach sampling was undertaken at these and six other breeding areas along the east coast of the South Island, New Zealand: Moeraki (45°20′S, 170°40′E), April –August 1984; Shag Point (45°20′S, 170°40′E), May – August 1984 and December 1984–July 1985; Bobbys Head (45°30′S, 170°35′E), March–August 1984; Penguin Bay & Hina Hina Cove (= Catlins) (46°30′S, 169°34′E), May & August 1984 and March 1985; and Falls Creek (46°30′S, 169°18′E), May 1984 and March 1985.

Breeding groups of this species are small, (5–7 breeding pairs at Shag Point, 9–17 pairs at Boulder Beach), so to minimise disturbance I visited breeding areas once monthly, except for Nugget Point (35–50 pairs) which was visited twice monthly. Penguins were caught as they came ashore at dusk.

Stomach contents were obtained using the water-flushing method (Wilson 1984). Two flushes were usually adequate to clear the stomach of its contents. The presence of small stones in the vomit confirmed that the entire contents had been flushed, as stones rest on the bottom of the stomach. Two to seven birds were sampled per evening. All penguins caught were weighed and banded. During breeding, adults were fed with blue cod (*Parapercis colias*) or yellow-eyed mullet (*Aldrichetta forsteri*) after flushing to ensure that offspring did not miss a meal. Samples were stored fresh and sorted the following day, or frozen until sorted.

Sorting techniques. Intact prey items were rarely encountered. These were measured and weighed. Loose otoliths (sagittal) were separated into left- and right-hand side, and dried at room temperature. Otolith pairs recovered from skulls were dried separately as a pair. When numbers of left- and right-hand otoliths of any one species in a single stomach differed, the number of prey in the stomach was taken as the larger number of the two. Otoliths were identified using the reference collection of Lalas (1983) and weighed. When large numbers of otoliths were present in one stomach (i.e., >50), otoliths were clumped into groups of not more than 20 similarly-sized individuals, weighed, and a mean value calculated for each size group.

Estimation of stomach contents. Fish lengths (total) and weights were estimated using the allometric equations of Lalas (1983), which relate otolith-pair weight to fish length, and fish length to fish weight. Cephalopod beaks were identified, measured (upper rostral length), and the allometric equations of Lalas (1983) applied to determine squid weights. All beaks showing excessive breakage or erosion were treated as being not from that day's foraging (van Heezik & Seddon 1990), and were excluded from the estimated stomach composition. A study of beak digestion in yellow-eyed penguins showed that all beaks had broken and abraded wings after 24 h, and after 36 h all surfaces were smooth and rounded (van Heezik & Seddon 1990). Relative to fish, the amount of squid in the diet is likely to be slightly overestimated; however, yellow-eyed penguin stomachs did not contain large numbers of beaks, and so a correction factor was not ascribed. Meal weights were estimated from the combined calculated weights of all prey species.

Contribution of each species to the diet was expressed as a mean percentage of the total calculated meal weight ingested of all stomachs sampled, mean percentage of the total number of prey items identified, and mean percentage frequency of occurrence (number of stomachs containing the species as a percentage of the total number of stomachs sampled).

Measurements of the horizontal relaxed gape of the penguins were made using Vernier calipers (accurate to ± 1mm), in order to relate gape width to sizes of prey items consumed.

Seasons are defined as follows; autumn (March–May), winter (June–August), spring

(September–November) and summer (December–February).

RESULTS

Prey species. The mean contributions of prey species in the diet of the yellow-eyed penguin from all seven breeding areas are shown in Table 1. Six fish and one squid species made up 94% of the weight and 97% of the number of prey items. None of the remaining 20 taxa made up more than 1% of the diet by weight. The diet of juveniles differed from that of adults in that it contained less fish and more squid by weight (χ^2=36.0, d.f.=1, P<0.001), (Table 2).

The percentage frequency of each length class for each season are plotted for red cod (*Pseudophycis bachus*), opalfish (*Hemerocoetes monopterygius*), sprat (*Sprattus antipodum*), silversides (*Argentina elongata*), and ahuru (*Auchenoceros punctatus*); and each weight class for arrow squid (*Nototodarus sloanii*) (Fig. 1). Most prey were less than 200 mm long, although opalfish consumed were up to 350 mm long. Most squid eaten weighed less than 100 g. The mean relaxed horizontal-gape of yellow-eyed penguins was 34 mm (SD=2.2, n=187). Regression equations relating total fish length (x) to maximum body depth (y) are: red cod, y=0.191x −1.0114, (n=11, r=0.985); opalfish, y= 1.104 + 0.095x, (n=13, r=0.991). The figure for the mean relaxed horizontal-gape of yellow-eyed penguins is about the same as the maximum body depth of an opalfish of 360 mm, and a red cod of 180 mm total length.

Inter-locality variation in diet composition. Percentage contributions in terms of weight and percentage occurrences of the seven principal diet species were calculated for each of the seven breeding areas (Fig. 2). This combination of seven prey species comprised at least 87% and as much as 95% of the total calculated weight at all breeding areas. Sprat occurred in 61–84% of all stomachs from everywhere except Boulder Beach, where it was found in 49% of the total. Opalfish, red cod, and squid were found at all breeding areas in at least 23%, and as many as 65%, of the samples.

Variation in diet between the 1984/85 and 1985/86 seasons. The 1985/86 season was identified as being one of poor reproductive success (van Heezik & Davis 1990). Fledging weights were significantly lower at Nugget Point in the 1985/86 season (1984/85; $\bar{x}$=5.62 kg, SD=0.59, n=24, range, 4.3–7.1 kg, 1985/86; $\bar{x}$=4.12 kg, SD=0.96, n=15, range, 2.25–5.55 kg, t=6.1, P<0.001), but were not

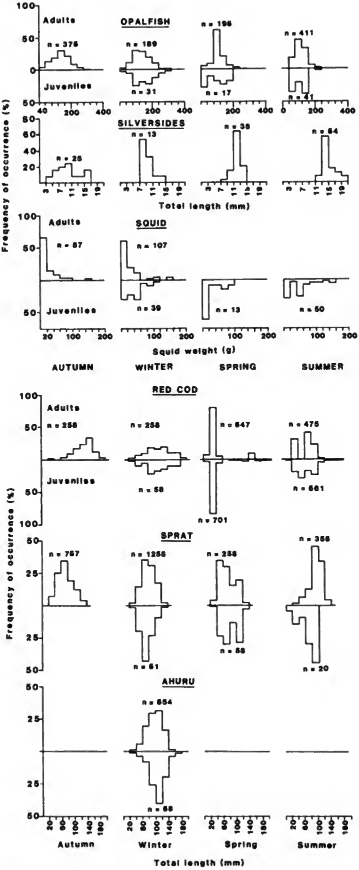

Fig. 1 Size-frequency distributions (percentage of total) of six prey species of the yellow-eyed penguin. Adult yellow-eyed penguin intake is shown above the x axis and juvenile yellow-eyed penguin below.

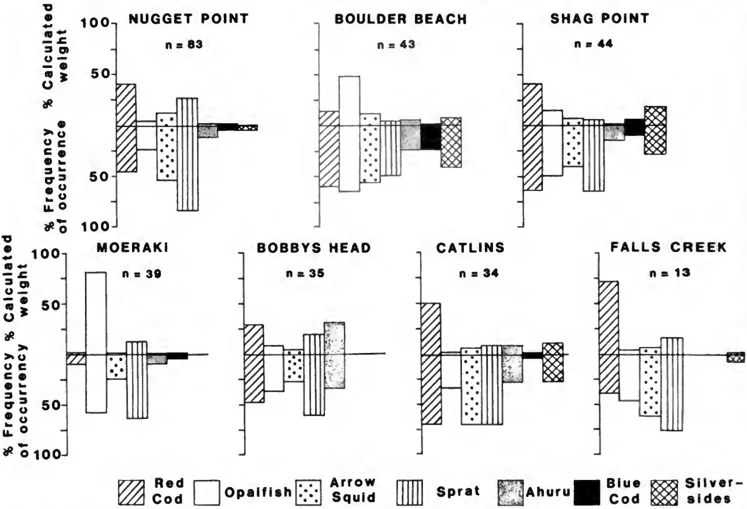

Fig. 2 Diet composition of adult yellow-eyed penguins at seven breeding areas, over one year of sampling. Numbers of penguins sampled are given as *n* values. Number of sampling dates are as follows: Nugget Point (21) Boulder Beach (9) Shag Point (11) Moeraki (7) Bobbys Head (7) Catlins (3) Falls Creek (2).

Table 1 The food of 512 adult yellow-eyed penguins from seven breeding areas on the Otago coast.

Principal species		**% Caculated Weight** X	SD	**% Numbers** X	SD	**% Occurrence** X	SD
red cod	*Pseudophycis bachus*	36	22	34	21	47	20
opalfish	*Hemerocoetes* spp.	22	30	15	16	44	15
arrow squid	*Nototodarus* sp.	9	7	3	2	47	18
sprat	*Sprattus antipodum*	12	6	28	15	67	11
ahuru	*Auchenoceros punctatus*	7	11	11	14	17	11
blue cod	*Parapercis colias*	2	3	1	1	6	8
silversides	*Argentina elongata*	6	7	5	6	15	16

Occurring occasionally—barracouta *Thyrsites atun*, cockabully *Trypterygion* spp., warehou, *Seriolella brama*, ling *Genypterus blacodes*, tarakihi *Nemadactylus macropterus*, hoki *Macruronus novaezelandiae*, rattails Macrouridae, hake *Merluccius australis*, giant stargazer *Kathetostoma giganteum*, N.Z. sole *Peltorhamphus novaezeelandiae*, long-snouted pipefish *Stigmatophora macropterygia*, seahorse *Hippocampus abdominalis*, silver conger eel *Gnathophis habenatus*, short-finned eel *Anguilla australis*, lamprey *Geotria australis*, warty squid *Moroteuthopsis ingens*, octopus *Octopodidae*, cuttlefish *Cephalopoda*, squillid shrimp *Heterosquilla* spp., salps Thaliacea.

significantly different at Boulder Beach (1984/85; x=4.94 kg, SD=0.45, n=11, range, 4.25–6.20 kg, 1985/86; x=4.83 kg, SD=0.67, n=18, range, 3.6–6.1 kg, t=0.5, P>0.05). At both breeding areas the range of weights included very light birds (<4.0 kg), and this was reflected in lower recovery rates of these fledglings as juveniles; <1% from 1985/86 compared to 26% from 1984/85 at Nugget Point, and <1% from 1985/86 compared to 18% from 1984/85 at Boulder Beach. At Nugget Point 18% of chicks starved to death.

Table 2 Composition of juvenile (82 stomachs sampled) compared with adult (512 stomachs sampled) yellow-eyed penguin diet.

	% Caculated weight		% Occurrence	
	Juvenine	Adult	Juvenile	Adult
arrow squid	49	9	44	47
red cod	29	36	58	47
blue cod	7	2	5	6
sprat	3	12	59	67
ahuru	3	7	27	17
silversides	3	6	7	15
opalfish	2	22	39	44
miscellaneous	4	6	32	39

Three kinds of fish and arrow squid made up most of yellow-eyed penguin diet between March 1984 to July 1985 at Nugget Point, and August 1984 to July 1985 at Boulder Beach, whereas in the following year (August 1985 – August 1986 at both breeding areas) the proportion of the three fish species decreased, whereas squid, blue cod and miscellaneous groups increased (Table 3).

A comparison of the two breeding seasons showed a trend of decreasing principal fish species and increasing proportions of other prey, in particular, arrow squid (Table 4, Fig. 3). Significant differences were found between the absolute quantities of most of the principal prey species or prey groups consumed in each breeding season. During a particular year there were also significant seasonal fluctuations in relative intake of various species (Fig. 3). Between early 1984 to mid-1985 sprat, opalfish, and miscellaneous species intake varied significantly at Nugget Point (Kruskal-Wallis, d.f.=12, H=23.3, H=34.5, H=44.1, P<0.05, respectively) and red cod, sprat, and opalfish varied significantly at Boulder Beach (d.f.= 7, H=19.2, H=27.1, H= 25.6, P<0.05, respectively). There was no significant difference in the relative intake of squid throughout the year at either breeding area.

Table 3 The percentage contribution of each prey species to the intake (biomass) of the yellow-eyed penguin over two years, and over two seasons (Dec–April).

% Calculated weight	year 1		year 2		P	breeding season 1		breeding season 2		P
Nugget Point										
red cod	45	66	41	46	* Z=72	52	88	13	16	** Z=146
sprat	18		4			30		2		
opalfish	3		1			6		1		
ahuru	17		2			<1		<1		
blue cod	1		8			0		10		
squid	10		34			12		63		
miscellaneous	6		11			<1		12		
Boulder Beach										
red cod	15	77	3	49	* Z=70	17	93	3	29 Z=100	**
opalfish	53		32			65		23		
silversides	9		14			11		3		
blue cod	2		9			3		6		
squid	15		30			4		56		
miscellaneous	5		12			1		7		

Year 1 (Nugget Point) = March 1984–July 1985, (Boulder Beach) = August 1984–July 1985
Year 2 (both breeding areas) = August 1985–August 1986.
breeding season 1 = Dec–April 1984/85, 2 = Dec–April 1985/866.
*differences between proportions tested following Zar (1984); * = P<0.05, ** = P<0.01.

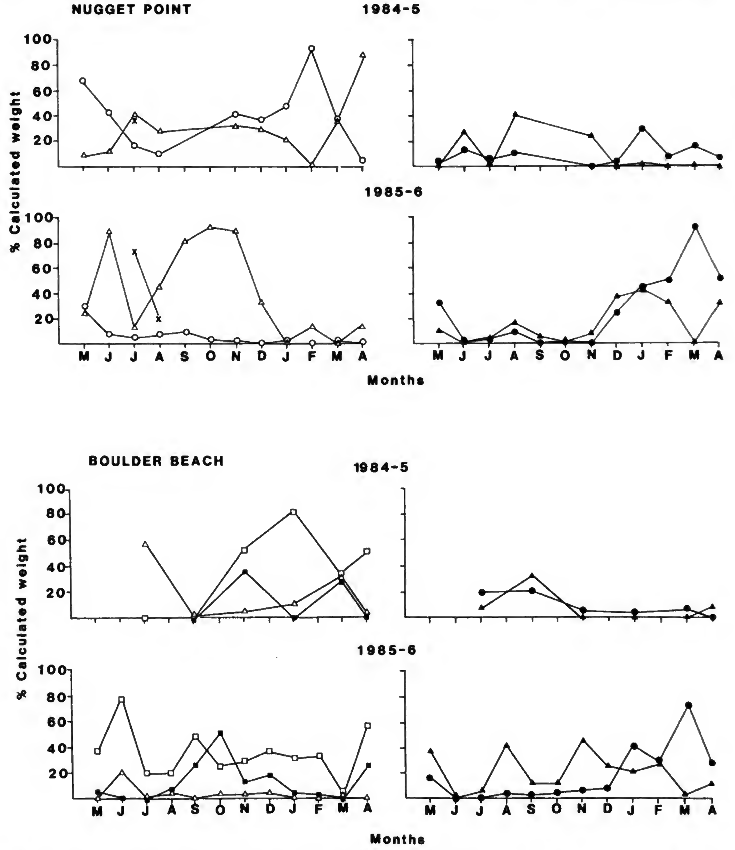

Fig. 3 Percentage contribution to the total calculated intake (weight) of yellow-eyed penguins over two seasons: (1) 1984/85: (2) 1985/86 at two breeding areas: (a) Nugget Point; (b) Boulder Beach, of six prey items: (open circle) sprat; (open triangle) red cod; (closed circle) arrow squid; (closed triangle) miscellaneous group; (open square) opalfish; (closed square) silversides; (cross) ahuru.

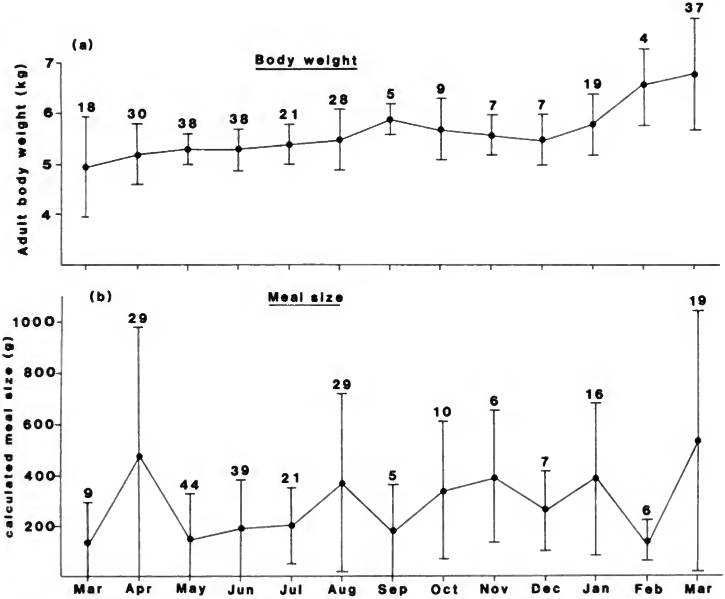

Fig. 4 Monthly means, from all study areas combined, of (a) body weight and (b) meal size of yellow-eyed penguins, ± one standard deviation. Sample sizes are given.

Table 4 Mean weights (calculated) of prey species from yellow–eyed penguin stomachs sampled at two localities during two breeding seasons (December–April). Quantities tested for significance using the Mann–Whitney μ test

	Nugget Point			Boulder Beach		
	Mean stomach weight(g)			Mean stomach weight(g)		
	1984/85	1985/86		1984/85	1985/86	
Species	n=31	n=66	P	n=14	n=24	P
red cod	137	85	ns	102	33	*
sprat	62	11	***	–	–	–
opalfish	–	–	–	402	228	*
silversides	–	–	–	67	34	ns
blue cod	0	68	–	–	–	–
squid	42	421	***	163	424	*
miscell.	6	128	***	18	117	*

*=P<0.05; ***=P<0.001.

Body weights and daily adult intake. Mean adult body weight was 5.5 kg (n=256, SD=0.70) and was heavier than the mean juvenile (first year birds) body weight of 5.1kg (n=96, SD=0.70), (t=4.2, d.f.=352, P<0.05). Mean adult body weights fluctuated significantly throughout the year (Fig. 4),(Kruskal-Wallis, H=53.3, d.f.=12, P<0.05). Variation in adult body weights between localities was also significant (Fig. 5), (Kruskal-Wallis, H=14.7, d.f.=4, P<0.05).

The mean calculated adult meal size was 340 g (n=281, SD= 390), 6% of the mean adult body weight. No significant variation was found in meal size throughout the year (Fig. 4), (Kruskal-Wallis,

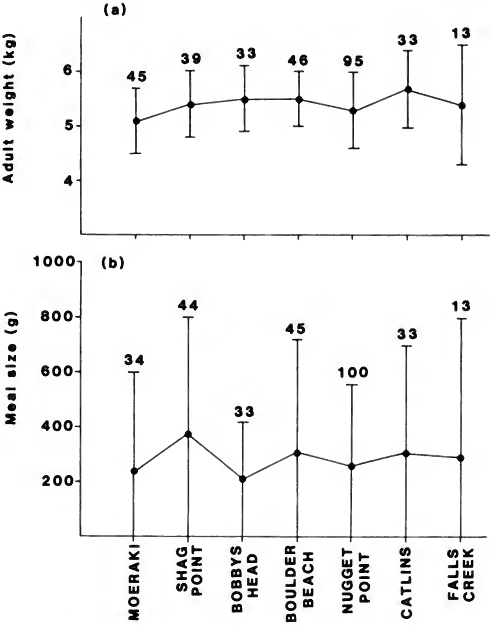

Fig. 5 Yellow-eyed penguin mean adult body weights (a), and mean meal weights (b) ± one standard deviation, at seven breeding areas: MO – Moeraki; SP – Shag Point; BH – Bobbys Head; BB – Boulder Beach; NP – Nugget Point; CA – Catlins; FC – Falls Creek. Sample sizes are given.

H=20.9, d.f.=12, 0.10 >P>0.05), but meal size did vary between breeding areas (H=27.1, d.f.=5, P<0.05), (Fig. 5).

Of the 281 adult stomachs, 3% were empty and 5% contained more than 20% of mean adult body weight (=1100 g). Otoliths of the heavy samples showed minor signs of erosion only, indicating they had been in the stomach less than 1 day (van Heezik & Seddon 1990).

Mean juvenile meal size was 366 g (n=59, SD=648), 7% of the mean juvenile body weight, and was not significantly different from mean adult meal size (t=0.4, d.f.=338, P>0.05). The standard deviation of juvenile meal size was larger than that for adults, indicating a wider range of meal sizes were taken by juveniles. Of 66 juveniles 3% were empty and 7% contained meal sizes of a weight equal to more than 20% mean juvenile body weight.

DISCUSSION

Diet composition. Twenty-six prey species were found, with fish comprising about 85% of the calculated weight and 94% of the total number of prey items. Sprat occurred in the largest number of stomachs sampled (70%), with red cod, opalfish, and arrow squid occurring in just under half. Although squid were taken in small quantities throughout much of the first 18 months their contribution was possibly overestimated as beaks can be retained undamaged for periods longer than a day (van Heezik & Seddon 1990). The relatively higher quantities of squid eaten in the second season was not because of large numbers of small beaks; rather, a few large individuals were often regurgitated almost intact. Hence, the increase in squid consumption was not caused by increased retention of large numbers of beaks. Conversely, rapid digestion of small otoliths ingested early in the foraging trip may result in an underestimation of fish species with small otoliths, i.e., sprat and small opalfish. Planktonic krill were absent from the diet, even though *Munida gregaria* and *Nyctiphanes australis* are abundant in the area north of 46°30′S, although not in every year nor continuously throughout each year (Zeldis 1983; Murdoch 1985). The juvenile diet differed from that of adults in that squid comprised the largest portion of the biomass (47%), but meal size was similar. Very few adult and juvenile penguins had empty stomachs.

Prey size. Fish larger than 200 mm were seldom taken. Opalfish as long as 300 mm were captured, but this species is more slender than other prey, and longer individuals could be ingested whole. In many fish-eating birds that swallow their prey whole, it is the width of the gape rather than the length of the bill that restricts ingestion of large prey (Swennen & Duiven 1977; Hulsman 1981). Hence, it is the maximum depth of the fish's body rather than its length that determines whether it can be swallowed. Slightly larger individuals will be able to be swallowed when the beak opens wide and the width of the gape is stretched. In yellow-eyed penguins the mean relaxed gape size corresponded to opalfish of about 350 mm length and red cod about 180 mm long, values close to the maximum size of each of these prey species taken by yellow-eyed penguins.

Yellow-eyed penguins were feeding on adult opalfish, sprat, and ahuru, juvenile silversides and arrow squid, and 0+ year class red cod (Ayling & Cox 1984; Mattlin et al. 1985), (Fig. 1). Juvenile yellow-eyed penguins took relatively less fish than adult penguins, but the sizes of prey in diets of juveniles were similar to those in adult diet. In spring, most red cod found in stomachs were postlarval (20–60 mm length) individuals from the previous winter's spawning.

Prey distribution. All prey species eaten are found over the continental shelf: sprat, ahuru, silversides, juvenile arrow squid, and young red cod are all mid-water species, opalfish are distributed demersally, and blue cod are common over and near rock reefs (Ayling & Cox 1984; Mattlin et al. 1985). Juvenile arrow squid are most abundant towards the surface, i.e., at depths of 50–100 m, where they have been found to represent 47% of the total commercial squid catch (Mattlin et al. 1985). This suggests that yellow-eyed penguins forage over the continental shelf, mainly from the upper portion of the water column, but also demersally (see also Seddon & van Heezik 1990).

Feeding appears to occur away from the coast, as shallow coastal-fish species common in marine shags (Lalas 1983) are absent in the diet of yellow-eyed penguins, even though penguins and shags nest in the same areas. The brief appearance of ahuru in the diet in winter may reflect a short period of inshore feeding, although it may also because of a change in the distribution of ahuru, which may move further off the coast during spawning.

Variations in diet composition. Seasonal and inter-locality differences in body weight, meal size, and reproductive success may be caused by variations in diet composition. Adults in this study gained weight before egg-laying and then slowly lost weight during the incubation and guard phases of the breeding cycle (Fig. 4).

Changes in adult body weight were not paralleled by changes in meal sizes, indicating that other factors also play a role in determining body condition, such as frequency of feeding, the effort required to capture food, physiological demands associated with feeding offspring or moulting, and meal composition. When feeding frequencies of breeding adults were lower, (in October and November incubating birds undergo unrelieved spells at the nest ranging from 1–7 days; Seddon 1989), meal sizes tended to be relatively larger. In January some non-breeding adults begin to gain weight in preparation for moulting. High body weights in February and March are of pre-moult adults. The physiological demand of a 40% weight gain before moulting is accompanied by larger meal sizes than at any other time. Daily intake amounting to 45% body weight was observed in captive jackass penguins *Spheniscus demersus*, 1–2 weeks before visible signs of moulting, and after completion of the moult (Gailey-Phipps & Sladen 1982).

Meal composition varied seasonally and between breeding areas. Consumption of some species was not continuous throughout the year; e.g., ahuru only appeared in the diet in July and August. Between breeding areas principal species remained the same, but the percentage contribution of each of these species to the total biomass differed (Fig. 2). However, sprat was found consistently in the largest proportion of stomachs at all breeding areas except Boulder Beach; opalfish, red cod, and squid appeared consistently in samples from all breeding areas, and made up a larger part of the diet during the months of chick feeding and moult.

A comparison of two seasons of contrasting reproductive success (1984/85, 1985/86) showed that the combined proportion of the three principal fish species decreased from 88% to 16% at Nugget Point, and from 93% to 29% at Boulder Beach (Table 3). However, meal sizes were heavier in the second season (Table 4), with the difference being made up by a large increase in the amount of squid (from 12% to 63% at Nugget Point, and 4% to 56% at Boulder Beach), as well as increases in blue cod at Nugget Point and miscellaneous species at both localities. Quantities of sprat were smaller in 1985/86 at Nugget Point, and red cod and opalfish at Boulder Beach. Larger quantities of squid, blue cod, and miscellaneous species were eaten at Nugget Point and Boulder Beach. During the second season it was not so much an absolute food shortage as a shortage of certain prey items.

Prey species and diet quality. Sprat is an oily fish and provides a richer energy source than opalfish or red cod. The presence of fat increases the caloric value of fish considerably (Johnson 1920), and the northern sprat *Sprattus sprattus* has been shown (Harris & Hislop 1970) to have the highest caloric values of any of the species eaten by puffins (*Fratercula arctica*). Harris (1984) found puffins grew best on oil-rich fish, and Gailey-Phipps & Sladen (1982) suggest that the fat content of fish is important in diets of captive penguins, as health problems occur when penguins are kept on low-fat diets. Seasons of abundant sprat in yellow-eyed penguin diet may result in high fledging weights and optimal growth rates (e.g., Nugget Point 1983/84 and 1984/85 seasons, van Heezik & Davis 1990), whereas low quantities of sprat may result in depressed growth rates and starvation. The value of sprat is also indicated by its high frequency of occurrence in all stomachs sampled. Arrow squid and red cod are of low oil content (Vlieg 1984a, b). A diet of squid resulted in slow growth, low fledging weights, and poor plumage development when fed to jackass penguin chicks (Heath & Randall 1985).

High caloric values of sprat may also explain the larger inconsistencies between mean meal size and adult body weight at two of the breeding areas; at Bobbys Head meal sizes were low but body weights were high, possibly because 20% of the intake consisted of sprat. At Shag Point, meal size was highest but body weights less than average, and diet consisted of opalfish and juvenile red cod and silversides, which are likely to be of low caloric value since fat content of other species has been shown to be less in juvenile forms (Harris 1984). That squid has a lower nutritional value is also suggested by lower body weights of juvenile penguins, which eat proportionately more squid and less fish.

Selective or opportunistic feeding. Certain characteristics of foraging indicate that yellow-eyed penguins are more likely to be selective than opportunistic: (1) only seven species comprise between 87–98% of their total intake over all mainland breeding areas sampled; (2) krill was not eaten; (3) the absence of inshore species; (4) the low mean number of species recovered from any one meal; and (5) the difference in diet between adult and juvenile penguins. Juvenile pelicans *Pelecanus occidentalis* (Brandt 1984) and juvenile jackass penguins (Wilson 1985) have been identified as being less efficient foragers than adults. Juvenile jackass penguins are not able to swim as fast as adults, rendering certain species of prey unavailable to them. The time that juvenile yellow-eyed penguins spend at sea after leaving the natal breeding area is also the period of highest mortality (Richdale 1957), and even after returning to land their weight is lower than adult weight. Juveniles may be forced to spend as much time feeding as possible, and be less selective than adults in their choice of prey.

Penguin diet and fisheries. Seabirds and industrial fisheries may exist in direct competition for pelagic fish (Furness 1978; Furness & Cooper 1982; Duffy 1983). The overexploitation of pelagic fish stocks by the commercial purse-seine fishery has been suggested as being responsible for declining jackass penguin numbers, as jackass penguins are selective in their choice of prey (Crawford & Shelton 1978; Randall & Randall 1986). The selectivity of the yellow-eyed penguin also makes it vulnerable to decreased availability of its principal prey species. Red cod and arrow squid are fished commercially off the east coast of the South Island. However, interactions between penguins and fisheries are complex, and competition between seabirds and fisheries cannot be invoked to explain changes in seabird numbers until the competition mechanism has been examined (Duffy et al. 1987). The inference that penguins are competing with fisheries because they take large amounts of a commercially exploited species need not necessarily apply (Duffy et al. 1987). The reduction in sprat and opalfish consumption observed in this study was not directly attributable to fishing, as they are not commercially exploited species in this region. A reduction in consumption may not be caused by a decrease in prey population numbers, but may result from a natural change in the availability of these species. The increasing incidence of breeding seasons of poor reproductive success indicate feeding conditions may have changed since Richdale's study (1957) during the years 1936–1954. More information on prey populations and interrelationships between trophic levels within the marine system is required before any cause-effect conclusions can be made concerning the impact of commercial fisheries on reproductive success.

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An analysis of the distribution and relative abundance of moa species (Aves: Dinornithiformes)

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Abstract Contributions to the understanding of moa ecology are reviewed. The distribution and relative abundance of each moa species in natural and archaeological sites is examined in detail. Eleven moa species (three dinornithids and eight emeids) are recognised in this study. The three dinornithids each had a New Zealand wide distribution. *Dinornis giganteus* primarily had a lowland distribution that coincided with areas suggested to have been vegetated in open low forest or shrubland. It was rare in wet, dense tall forests where the medium sized *D. novaezealandiae* was the dominant dinornithid. *D. struthoides*, the smallest dinornithid, ranged from lowlands to subalpine areas and was most abundant in forested areas. Among the emeids *Anomalopteryx didiformis* and *Euryapteryx geranoides* had a New Zealand wide distribution, *Euryapteryx curtus* and *Pachyornis mappini* were North Island endemics, and *Pachyornis australis*, *P. elephantopus*, *Emeus crassus*, and *Megalapteryx didinus* South Island endemics. *Anomalopteryx didiformis* was primarily an inhabitant of wet lowland, tall podocarp-broadleaf forests. Both *Euryapteryx* species and *Emeus crassus* were lowland inhabitants of shrubland or open low forests, and thus predominated in drier regions. *Euryapteryx curtus* and *Emeus crassus* may have been ecological equivalents. In the South Island *Euryapteryx geranoides* seems to have preferred areas postulated to have been clothed in dry inland low forests generally over 200 m above sea level. *Emeus* seems to have had a predominantly coastal distribution. *Megalapteryx didinus* primarily inhabited upland areas of montane to subalpine habitats. *Pachyornis mappini* was a lowland species with an affinity for wetlands. It was rare in areas of continuous tall forest and most common where a shrubland-forest mosaic existed. *P. elephantopus* was the South Island equivalent of *P. mappini* but was absent from continuous areas of wet tall forests. *P. australis* replaced *P. elephantopus* in montane forests and subalpine areas, apparently preferring wetter colder areas. This analysis shows patterns of distribution that are correlated with differing vegetation types so allowing general habitat preferences to be determined. Each species clearly had a distinctive habitat preference that suggests that usually only three to four species coexisted in any one habitat, niche separation being effected by differing sizes and beak morphologies. It is no longer acceptable to refer to moa ecology without qualification by taxa concerned.

Keywords Moas; Dinornithiformes; species distribution; relative frequency; ecology, habitat

INTRODUCTION

The moas (Aves: Dinornithiformes) are giant extinct birds that formerly inhabited New Zealand. Since the discovery of their bones by Europeans in 1839 they have excited the scientific community and caught the imagination of the general public. In the 150 years since 1839, papers on their taxonomy have proliferated (see Archey 1941; Cracraft 1976; Worthy 1988a); yet, despite this, the taxonomy, until recently, still requires amendment (Worthy 1988b, 1989a, 1989d).

The confused taxonomy of the past, combined with the large number of described species may account for our poor biological understanding of the various moa species. As we shall see, most authors when venturing comments on habitat, etc. have

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generalised by including all moa species, ignoring the diversity of the group and all that implies for ecological niche differentiation.

Some specific aspects of the biology of moas, for example locomotion (Alexander 1983a, 1983b) and diet (see later section), have been examined before. In this paper I attempt a generalised reconstruction of the ecology of each moa species.

I will first review those statements that have resulted in the current ideas of moa ecology. Few original ideas have been proposed; most authors merely repeat previous statements with minor variations.

Review of comments on the ecology of moas

Richard Owen, who awakened the scientific world to the existence of the Dinornithiformes in 1839, published the first species descriptions (Owen 1844) and within this (repeated in Owen 1879) he made the first suggestion as to the habits of moas.

> "Some at least of the characters of the skeleton of the *Dinornis* may well have related to rhizophagous habits. The unusual strength of the neck indicates the application of the beak to a more laborious task than the mere plucking of seeds, fruits, or herbage.... the still more robust proportions of their cervical vertebrae, and especially of their spinous processes, - so striking when contrasted with the corresponding vertebrae of the Ostrich or Emeu, - may well have been the foundation of those forces by which the beak was associated with the feet in the labour of dislodging the farinaceous roots of the ferns that grow in characteristic abundance over the soil of New Zealand."

Most researchers concerned themselves with identifying the taxa represented by the bones and thus revealing the diversity of form represented among moas. Julius von Haast, one of those tireless early workers, commenced recording his findings in the early 1860's. He worked primarily in the Canterbury region and was thus most familiar with the limited range of very impressive taxa found in that area. Impressed by the bulk and stoutness of these taxa, he ventured a comment on their likely habitat (Haast 1872: 73) which dominated subsequent speculation.

> "Judging from the structural character of the different species of *Dinornis*, they must have inhabited the open country where such existed, and not the forested regions, where not only innumerable impediments to locomotion would have stood in their way, but where they also would probably have found little food suitable to them. In the term 'open' I include plains and hill-sides in the low lands covered with grass, fern, tutu (*Coriaria ruscifolia*), flax (*Phormium tenax*), and cabbage trees (*Cordyline australis*), and the subalpine regions,... Moreover, I have no doubt that the different species of *Dinornis*, like those of the *Apteryx*, were omnivorous,... "

The only other ecological comments last century were by Travers (1876) who presented a letter penned by John White purporting to contain information gained from Maori informants. However, this was in essence little different to the suggestions of Owen (1844) and Haast (1872).

The flurry of papers concerning moas continued until the early 1900's but all were concerned with taxonomy or the relationship of moa and man. No ecological data were presented.

In a popular book Buick (1931: 213) continued to promote Haast's suggestion, with some imagination:

> "It [moa] browsed upon the hillside grasses as the cattle do, and devoured leaves and berries when it could reach them. At the season of the year when the tawa, the karaka, and the matai trees were in fruit, the birds would penetrate into some of the tighter bush, but at all other times of the year it preferred the open spaces."

Direct data on the diet of two moa species was soon to become available supporting Buick's scenario. Moa bones were first discovered in Pyramid Valley swamp, Waikari, North Canterbury in 1938 and excavations over the next 2 years revealed many individual skeletons, including gizzard contents, in an excellent state of preservation that (Duff 1941) reported to contain seeds, grass, and other vegetable matter. Falla (1941) reported the analyses of two samples of gizzard contents by R. Mason to show that the last meal of *Emeus crassus* (XVIB) included 58 seeds of *Podocarpus spicatus* (matai), eight of *Myoporum laetum*, one of *Nertera* sp., and others of probably *Carmichaelia* and *Gaimardia* The other sample from *Dinornis* (XXIIK) contained about 200 seeds of *Coprosma rhamnoides* and a mass of twiggy material. It is probable that Duff expected to see grass and so misconstrued the fibrous twiggy mass as grass. Mason's analyses provided the first data on diet of a moa species, but it did not change the generally held opinion that moas were primarily open country birds. Archey knew of Mason's results yet in his monograph (Archey 1941: 81) he wrote:

> "It was in the latter extensive open grasslands of the South that the moa abounded, particularly the massive forms whose ungainly bulk would probably have caused them to favour the lowlands, leaving the higher tussock and scrub country to the more slender species, e.g., of *Anomalopteryx* and *Megalapteryx*, and probably of the tall *Dinornis* also,.. "

However, this statement is significant as for the irst time there is allusion to the fact that some taxa ccurred in one habitat and others elsewhere. But rchey was unwilling to entertain the concept of a oa species being principally a forest inhabitant. In onsidering their habitat he (p. 91) reverts to "the noa":

> "Another adverse factor [relating to their extinction] may have been the extension of the forest during the pluvial period. It is well known that **the moa** penetrated into the forest—**they** were entrapped in caves far into the bush;.. Possibly they wandered in in search of food, but bred in more open situations." (bold - mine).

Despite this, Archey's observations led him to comment on habitat preferences; he suggested *Megalapteryx* was possibly a high country species (Archey 1941: 35). Similarly he noted that *A. didiformis* occurred throughout New Zealand but chiefly in hilly country (Archey 1941: 29). Oliver (1949: 181) concluded that the moa lived mainly in open country and frequented swampy places, but that it probably did not go far into the forest. He did not expand upon the idea first mooted by Archey of differential habitat utilisation.

In 1949 Roger Duff wrote "Pyramid Valley—the story of New Zealand's greatest moa swamp." It was reprinted in 1952 and the same material was used for "Moas and moa hunters", first published in 1951 and reprinted in 1957, which was widely disseminated in schools. These popular booklets, while acknowledging the dietary data presented by Falla (1941), promoted the idea that grassland was the preferred habitat.

> "Of them all, the moas were the closest equivalent of the hoofed stock now grazing on our pastures. The largest variety (*Dinornis maximus*).. probably required as much grass each day as a bullock."

However, Duff (1951) did acknowledge Archey's comments about *Anomalopteryx* and *Megalapteryx* and referred to these genera as forest dwellers. But usually Duff's over-riding tendency was to generalise and state the moa did this etc., with no reference to interspecific variation.

Falla (1962) was more specific, and after repeating Archey's suggestion that *Anomalopteryx* and *Megalapteryx* were presumably small bush moas, he noted that nothing much is known of the habitat or food preferences of *Pachyornis* and from the structure of *Euryapteryx* it was almost certainly a low country and probably a grassland and forest edge species.

So the net advance in understanding of moa ecology since Haast (1872) amounted to little more than the suggestion that *Anomalopteryx* and *Megalapteryx* were bush dwelling moas.

Scarlett (1957) outlined the distribution of different moa species but did not consider their relative abundance within the observed ranges nor did he comment on their probable ecology. Simmons (1968) reviewed information from botanical, zoological, geological, and archaeological sources and concluded that the moas were primarily inhabitants of forests, not grasslands. This paper was the first to present a strong cogent argument for any suggested habitat of the moa. However Duff's influence prevailed and Simmon's paper remained largely uncited. The understanding of moa ecology, as summarised by Duff (1952), was repeated by Scarlett (1969), Falla (1974), and Duff (1977). For example Duff (1977: 281) stated:

> "that the great grassland moas were flourishing in all their genera.. "

This last comment by Duff came after renewed investigations into moa remains at Pyramid Valley in 1965, reported upon by Gregg (1972). The contents of three gizzards were examined by Mason, one each of *Dinornis maximus*, *Euryapteryx gravis*, and *Emeus crassus*.

Briefly, the *Dinornis* gizzard contained fruit, leaves, and stems whereas that of the other two species contained only fruit and leaf material so Gregg (1972) concluded that these moas were browsing rather than grazing animals. This conclusion was obviously noted by Fleming (1974) who, when commenting on likely moa habitat, omitted all reference to grasslands and stated that they browsed on shrubs and trees of the forest margins. Even more recently the information presented by Falla (1941) and the unsubstantiated propositions of Duff (1952, 1957) were mixed by Stevens (1980):

> "Most of them [*Dinornis*] probably grazed grassland plains, shearing off the grasses with their massive beaks.. Many of the smaller moas lived in the forests, where they browsed on the twigs and leaves of many shrubs (e.g.,

> *Carmichaelia*) and low lying trees, such as ngaio (*Myoporum*) and the berries and fruits of trees (e.g., the podocarps, many of which have fleshy fruits.)"

At the time of publication of Steven's book a renewed research effort into the diet of moas was underway. Gizzard contents obtained during the Pyramid Valley excavations were studied by Burrows. After the initial study of a gizzard from a large *Dinornis*, Burrows (1980a) stated:

> "A general conclusion may be made that the larger moa, *Dinornis*.., *Emeus*.. and *Euryapteryx*.. habitually relied on twigs of woody plants as important items of diet."

But it is important to note that neither Falla (1941), who described contents from an *Emeus crassus* gizzard, nor Gregg (1972), who described the gizzard contents from an *Emeus crassus* and an *Euryapteryx geranoides*, made any suggestion of twigs being present, only berries and leaves. Burrows (1980b) reported on the gizzard contents of 14 moas. Because of unresolved taxonomic status of some moas only generic names were used and unfortunately measurements for the associated *Dinornis* skeletons were not given. However, those from Pyramid Valley were probably from *D. giganteus* which is the most common dinornithid at Pyramid Valley. The Scaifes Lagoon gizzards although "probably almost complete" (Burrows 1980b) are much smaller. Because Trotter (1970) records the following from Scaife's Lagoon "five part skeletons of *Dinornis torosus*, a part skeleton of *Dinornis robustus* and odd bones of *Dinornis maximus*", and because of the small volume of the gizzards collected, it is probable that these gizzards are from the smaller *D. torosus* (= *struthoides* this paper). Burrows (1980b) concluded:

> "These moas were browsing animals predominantly, but fed also on seeds and fruits. They sheared twigs off and ground them up in their large gizzards.... The habitat of the birds just before their death included the edge of podocarp-mixed angiosperm forest round the margins of mires, or open forest of this type."

But Burrows (1980b) did acknowledge that the diet of *Dinornis* probably was different to that of the other species for which information was available as he stated:

> "But *Emeus* and *Euryapteryx* may have relied more on seeds and leaves than did *Dinornis*"

The new data and all previous dietary data was summarised in a popular form by Burrows et al. (1981). They noted that bill shape differences indicated different feeding niches between species and that future study may show a greater dependence of *Emeus* and *Euryapteryx* on leaves and seed than on twigs. However, these same authors in their abstract lumped all three genera together stating:

> "There is evidence that **they** sheared off short pieces of twigs of the plants on which they were feeding."(bold – mine)

There is in fact only evidence for *Dinornis giganteus* and *D. struthoides* having eaten twigs. A conclusion, noted by Burrows et al. (1981) but overlooked by others, is that probably all the moas of Pyramid Valley and Scaifes Lagoon for which gizzards have been analysed were trapped between November and February. This contention is supported by the fruit and seeds of *Cordyline*, *Plagianthus*, *Prumnopitys taxifolla* (matai), *Coprosma rotundifolia*, *Corokia*, and *Melicope simplex* which were consistently present in the analysed gizzards. November to February (summer) is when these plants produce their fruit and is usually the driest time of the year. So apart from the attraction of food, water must be considered when inferring habitat preferences. That is, the various species of moa may have been around Pyramid Valley and Scaifes Lagoon because they preferred the habitat near the edge of mires, or they may have only been coming to drink, browsing en route to the water supply. Indeed, Burrows (1989) argued that most moas trapped at Pyramid Valley had been either wading in a shallow lake or walking on its dry bed. Low water levels in summer would make it more probable that a bird would become mired in summer whilst attempting to reach water than during the high water levels present at other times of the year. Also, outside summer months temporary sources of water are available, negating the need to approach larger lagoons. Another source of attraction to consider may have been wetland plants that may have been partially exposed by low water levels. However, the virtual absence of such plants from gizzards so far analysed does not support such an idea.

Hamel (1979) discussed the breeding ecology of moas and made brief comparisons with other ratites. She concluded that the limited direct and some circumstantial evidence suggested that moas were solitary nesters laying only one to two eggs.

A very significant contribution to the study of moa ecology was made by Anderson (1983a) who drew together data on climate, soils, past vegetation, and moa distribution from both archaeological and natural sources for the Otago region. Anderson considered that because any species could be expected n either natural or cultural deposits and that more han one species occurred at a time in any place indiated that there was no reason to attempt to distinguish listributional differences on a species or genus asis. Anderson treated all moas as a group to conclude:

> "The relative suitability of moa habitats can be summarised as follows. Closed beech forest was avoided, alpine and lowland grasslands were poor habitats and so too were the woodlands or forests in the higher parts of the lower hill country. The prime moa habitat seems to have been at or near the base of the ranges along permanent watercourses, usually in shady situations such as gorges or gullies open to the south, where dense mixed shrubland was the predominant vegetation but where remnant forest patches or forest fringe lay in close proximity."

My criticism of this is that if a large enough sample of moas is obtained from a site or an area, the whole range of moas known from the Island can be obtained, for example, Glenmark (Scarlett 1969). So a species list in itself obscures the relative abundance of each—I expect that three to four species were predominant in the region concerned. The lack of qualification as to the predominant species in the area (i.e., Otago) in this summary are shortcomings of this approach.

Since Fleming (1974), statements concerning moa habitat have swung in favour of forests. For example, McCulloch (1982) stated that "moas lived in and around forest margins." And Trotter & McCulloch (1984) stated, "the diet of the South Island *Dinornis* consisted mainly of twigs.. " However they meant the diet of *D. giganteus* and probably that of *D. struthoides*, but not *D. novaezealandiae* which is also found in the South Island. Anderson (1984) described moas as inhabitants of shrublands and forest margins. Greenwood & Atkinson (1977) when presenting their hypothesis of the evolution of divaricating plants in New Zealand as being the result of moa browsing, treated moas as forest inhabitants. Brewster (1987) refered to moas as forest or forest edge species but had nothing specific to say about any species.

Most recently Atkinson & Greenwood (1989) have examined some of the relationships between moas, in particular, moa browsing and plants. They demonstrated differences in beak morphology and size which they suggested were of primary importance in niche separation, which they considered necessary because of a perceived high degree of coexistence between different species. They accepted that most species were forest or forest margin inhabitants and argued that some species frequented the subalpine zone at least seasonally. Their principal thesis was that many New Zealand plants exhibit morphologies consistent with adaptation to moa browsing.

Detailed studies of the whole fauna and flora from cave deposits in the Oparara Valley, Karamea, northwest Nelson using a multidisciplinary approach has recently enabled Worthy & Mildenhall (1989) to comment on the habitat preferences of some moa species. The upland moa (*Megalapteryx didinus*) and the crested moa (*Pachyornis australis*) were found to be the predominant moas in a montane forest - subalpine scrubland habitat whereas the little bush moa *Anomalopteryx didiformis* and large bush moa *D. novaezealandiae* probably preferred wet dense lowland forests. We suggested that *Pachyornis elephantopus* primarily preferred open dry habitats. These conclusions were further endorsed by (Worthy 1989a) and (Worthy 1989c).

Also, I have (Worthy 1989e) presented biological observations relating to the proposed ecology of *Pachyornis elephantopus* and *Euryapteryx geranoides* and concluded that their preferred habitat was dry lowland mosaics of shrubland, grasslands and forests.

Summary

In the first century of moa research, few observations were made that could contribute to an understanding of moa ecology and the few statements made, e.g., by Owen and Haast, were often repeated. These were developed by Duff into the hypothesis that became widely accepted of moas being predominantly grassland birds. Data obtained from gizzard analyses, first in 1940, then 1972, but mainly in 1980 eventually changed the widely accepted hypothesis of "grassland moas" to one of "forest moas". Only recently has the data concerning associated species, relative proportions of species, and consideration of a wide range of palaeoenvironmental observations led to suggestions as to the preferred habitat of individual species.

It is the aim of this paper to expand this approach and establish the individuality of each of the 11 currently accepted moa species.

METHODS, TERMINOLOGY, AND LIMITATIONS

This paper outlines the distribution of each moa species and reveals trends in relative abundance within each area of their ranges mainly using data available in the literature, although some new data are introduced. The species of moa recognised follow Worthy (1988a) and where identifications or re-identifications are made criteria in this paper are used. Although similar to Cracraft (1976) the classification I use differs in that it recognises two families (Emeidae and Dininorthidae) in the Dinornithiformes.

When I use the term "moas" I refer to all known species. But sometimes I am more specific and then use the term dinornithid to mean moas of the genus *Dinornis*, or emeid to incorporate moas of the family Emeidae. Emeidae is equivalent to Anomalopterygidae of Archey (1941) and Oliver (1949) and includes all moas other than *Dinornis* species. For data from the majority of sites, I have necessarily had to rely on the published identifications for material. My own re-analyses of material has revealed that most workers have been unable to consistently and correctly differentiate leg bones of the North Island species *Pachyornis mappini* and *Eurapteryx curtus*, so my lists of MNI (minimum number of individuals) for sites differ from others. I have also adopted a conservative approach to bone identity and so believe many fragments are only identifiable to family, resulting in lower total MNI of identified species in some sites.

In this paper the last glaciation is referred to as the Otira Glaciation and is taken to end 14 000 years ago. Full glacial conditions prevailed from 25 000–14 000 years ago. From then until 10 000 years ago is the period of transformation from cold conditions to those similar to the present and is termed the late glacial. From 10 000 years B.P. to the present is here called the post-glacial, Holocene of some authors.

General vegetation reconstructions, mainly based on existing vegetation distribution supplemented by pollen analyses, are taken from the literature and compared with the moa distributions revealed. In this way coarse ecological preferences and primary moa species associations are proposed.

Common abbreviations used are as follows: NMNZ—National Museum of New Zealand; AIM—Auckland Institute and Museum; CM—Canterbury Museum.

Limitations of the fossil record

Moa bones are found in three types of deposit:

Aeolian deposits of dune sands or loess—dunes are generally coastal and limited in distribution and if acidic in nature bones are not preserved. Most dune formation relates to the present sea level and is thus late Holocene in age. The principal dune areas preserving bones are the far northern and eastern areas of Northland, Wairarapa Coast, and Southland. Loess occurs throughout the southern two-thirds of New Zealand, is mostly non calcareous, and thickest and most extensive in the drier, rain shadow areas of eastern South Island, Wairarapa, and Hawkes Bay. Bones are only found in calcareous loesses and, although often reported, are of poor quality and difficult to extract. Few are preserved in collections. Banks Peninsula and Cape Wanbrow are two principal sources of loess-derived bones. Most are undated but are probably older than dune fossils because most loesses are of glacial age. However, bones could become buried on hillslopes by loess redeposition and if so could be considerably younger than the loess itself. Bones preserved in both dune sands and loess are here assumed to usually have been deposited during the formation of the deposits, not later after the formation of stable soil horizons.

Usually such areas would have been vegetated in a mosaic of shrubland and grassland but occasionally low forests would be overwhelmed by, particularly, blown sand.

Swamp deposits—these are commonest in lowland areas and will preserve bone only if they are non-acidic. Most coastal swamps are late Holocene in age since stabilisation of the water tables followed achievement of the present sea level about 6 000 years ago. This is so for all dated Canterbury spring or swamp sites but should not be taken for granted. For example, the Tangatupura site in Hawkes Bay contained bones of Otira Glacial age (Worthy 1987). Unlike cave pitfall traps that may underlie a range of habitats, swamps and springholes are a specific habitat—they are wetlands and may present a forest edge, so birds trapped in such sites were probably attracted by either or both of these characteristics. This contrasts with cave pitfall traps where there is no attraction. Therefore, a swamp-trapped fauna need not wholly reflect the fauna inhabiting the countryside in which the spring or swamp is set. For example, a small lake in an area of otherwise continuous dense lowland forest probably had a different avifauna attracted to it, than that which occurred in the forest. In the same way as some rails are today attracted to such areas some moas probably were also. Swamp or spring sites may not always have this attractive capacity as small springs, for example, the Clevedon site (Appendix 3) may be too small to support wetland habitat and the only attraction might be drinking water. So small springs probably trap animals representative of the surrounding habitat and not species preferring wetland habitat or forest margins. This argument provides the most probable explanation for the differences between faunas from larger swamp sites and caves of similar age and that are geographically close to each other. For example, the fauna of Hamilton's swamp at Winton and the nearby cave faunas from Browns and Forest Hill in Southland have quite different proportions of moa species (see discussion under *Anomalopteryx didiformis*).

Swamp sites can be split into two categories:
i - shallow lake, e.g., Pyramid Valley, Glenmark, the newly discovered Cheviot site, and Poukawa. Fossil assemblages from such sites characteristically comprise partially articulated skeletons
ii- spring holes, e.g., Clevedon, Makirikiri, Enfield, Hamilton typically trap birds in the same place so that a jumbled profusion of bones results

Cave deposits—in New Zealand most caves are formed in limestone and marble. Karst is the term for a landscape characterised by underground drainage and landforms associated with this phenomenon, e.g., blind valleys, caves, etc. New Zealand has only limited areas of karstic calcareous rocks, described by Williams (1982), which severely restricts cave fossil distribution. The main karst area in the North Island is south of Auckland through to the Awakino River and centres on Waitomo Caves in the King Country. Minor areas occur in Northland, Hawkes Bay, e.g., near Wairoa, and at isolated localities in the Puketoi Range and near Martinborough in the southeast Wairarapa. In the South Island the major cave areas are in the north and west. Paparoa National Park partially includes the largest continuous lowland karst area in New Zealand but smaller areas occur near Karamea (in which Honeycomb Hill Cave is found), Patarau, Collingwood, Takaka Valley, and the Buller River. Marble outcrops extensively in three areas; Takaka Hill (originally totally forested), Mt Arthur, and Mt Owen, both of which have subalpine aspects. These last three locations are highly cavernous and thus have many fossil sites. Elsewhere in the South Island there are a few minor karst areas in Canterbury, Southland, and Fiordland although cave deposits in Southland are largely undescribed, for example Forest Hill. Fissure deposits are found in the schist areas of Otago but these are usually small and are relatively rare.

Although some New Zealand caves are known to be at least 700 000 years old (Lyons 1985) the oldest dated fossil from a cave deposit is 24 100 ± 450 y BP (Millener 1981: 848). The majority of dated cave remains have been collected from superficial deposits and are Holocene in age. Few excavations had been made until recently. Most karst features are relatively recent, especially in the shallow limestones of the East Coast regions of both the North and South Islands.

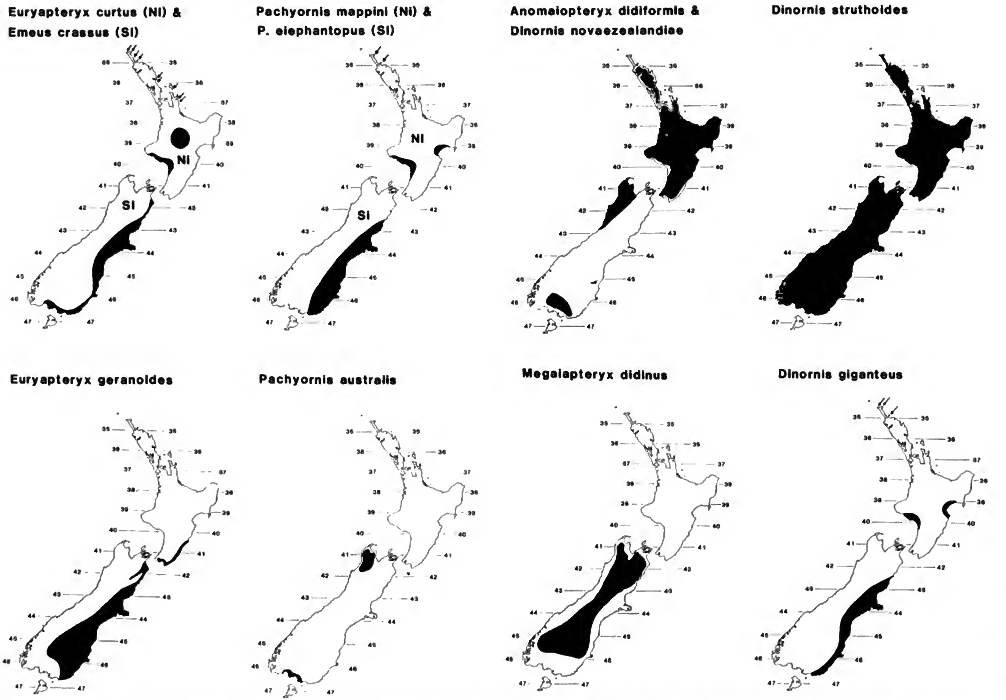
Caves trap the inadvertent passer-by, and their deposits reflect the ground fauna of the surrounding area. If special conditions prevail a significant component of the volant fauna can also be trapped, e.g., Eagles' Roost at Honeycomb Hill (Worthy unpubl. data). Caves with different sized entrance potholes are variably perceivable and so some are more effective traps than others. However, caves contrast with swamp sites which, because of their nature, attract then trap animals. Thus, I believe, caves provide a less biased sample of the prevailing fauna for an area. The distribution of caves predominantly in lowland, western areas where dense lowland podocarp broadleaf forests prevailed during the Holocene (McGlone 1985) provides extensive data on the fauna of these areas. The absence of extensive karst in the drier eastern rainshadow areas means that there are only a few cave sites, that are usually small, thereby limiting faunal records. Karst on Mt Luxmore and in Takahe Valley (Fiordland) plus Mt Owen and Mt Arthur (northwest Nelson) provide subalpine sites.

The distribution of a species in the fossil record mostly reflects available sites and, for many groundbirds in particular, mirrors the distribution of karst. When considering all types of fossil deposits it is not the gross distribution but the relative abundance of a given species within each site and its interspecific associations that will reveal information about its ecological preferences. Loess and dune sites, although restricted in distribution, provide a fauna from a particular habitat, i.e., relatively open shrublands, which were poorly represented in areas containing caves during the Holocene. Swamp or lake deposits sample birds attracted to wetlands. Thus an assessment of the fauna from all three types of deposits, in consideration with their limitations, should reveal something of the ecology of each moa species.

Definition of vegetation terms

The range of terms used to describe vegetation types include forest, low forest, scrub, shrubland, and grassland. To avoid confusion as to what I mean by these terms I define them here following the diagnostic criteria given by Atkinson (1985).

FOREST—woody vegetation in which trees dominate the canopy and which together with shrubs cover more than 80% of the ground surface. Trees are



Euryapteryx curtus (NI) & Emeus crassus (SI)

Pachyornis mappini (NI) & P. elephantopus (SI)

Anomalopteryx didiformis & Dinornis novaezealandiae

Dinornis struthoides

Euryapteryx geranoides

Pachyornis australis

Megalapteryx didinus

Dinornis giganteus

Fig. 1 Maps of New Zealand in which shaded areas show where the named species was one of the predominant moa species during the Holocene. Although fossil sites are only discrete points populations exist in areas so I have attempted to present maps of the areas both known and inferred to the significant for each species. The range of each species is wider than depicted and its limits are defined by the rare occurrance of specimens outside of the defined areas. Usually the range can be said to include virtually the whole of the island or islands inhabited. Latitude, as degrees South, is indicated by horizontal lines.

woody plants greater than 10 cm diameter breast height (d.b.h.).

SCRUB—woody vegetation in which shrubs (woody plants less than 10 cm (d.b.h.) dominate the canopy and which, together with trees, cover more than 80% of the ground.

SHRUBLAND—vegetation in which shrubs are the predominant growth form but do not form a semi-continuous canopy as in scrub.

GRASSLAND—vegetation in which the cover of grass (including tussocks) exceeds that of any other growth form, that is grass, sedge, or tussock cover is 20–100% of the canopy.

Pollen analyses of necessity assume that a given species is either a tree, a shrub, or a herb and thus the species composition denotes a vegetation type as defined above. Some species can however be shrubs or trees, for example, Kanuka (*Kunzea ericoides*), so interpretation of a vegetation type dominated by these is not unequivocal, but may be resolved by the presence or absence of other species. In previous studies the terms scrubland and shrubland have been used without definition and probably without distinction. So interpretation of what is meant by either of these terms in past studies is difficult but necessary as each present a quite different physiognomy. Similarly the term forest without some form of description may include vegetation types as different as one comprised of 6 m high kanuka trees to a rimu (*Dacrydium cupressinum*) forest with a canopy reaching over 60 m. I believe the structure of these vegetation types is all important in determining the suitability or otherwise to one or other moa species and that to a certain extent the specific composition of the vegetation types is secondary.

RESULTS

Distribution of moa species

In the following section the distribution and relative abundance in all types of natural deposit and in archaeological sites of each moa species, as recognised by Worthy (1988a), is reviewed. Fig. 1 shows the regions of New Zealand where the named species was a prominant component of the Holocene moa fauna in terms of its relative frequency to other members of its family. These diagrams do not show the range which more or less includes the whole of the island/s it inhabits. The data from which these maps we reconstructed are outlined for each species in the following section. Dinornithids are always much less abundant than emeids hence comparisons are only intra-familial.

***Anomalopteryx didiformis* (Owen)—Little bush moa**

NATURAL DEPOSITS. In the far north dune deposits bones of this species are rare (Millener 1981) yet within the same region are common in inland cave sites, e.g., Otangaroa (between Kaeo and Mangamuka) (Worthy 1985) and Waipu (Millener 1981). Elsewhere in the North Island it is common and the most frequently encountered moa species in the cave fossil fauna of the King Country, Ureweras, Hawkes Bay, Coonoor, and Martinborough areas (Millener 1981). Sites in these areas are presumed predominantly Holocene in age. In the swamp site of Poukawa in Hawkes Bay it is uncommon (17%—Worthy 1989d) being second in abundance behind *Pachyornis mappini*. *A. didiformis* dominated the late Holocene fauna in a lowland swamp at Clevedon, South Auckland (Millener 1981). Likewise it was the most common species in the mudhole at Makirikiri, near Wanganui (Archey 1941; Appendix 3) and the swamp site at Manakau, north of Wellington, both argued to be of Holocene age (Worthy 1989d). It was however rare at Te Aute (Hamilton 1889) and absent at the swamp site at Tangatupura, both considered of Otira Glacial age (Worthy 1989d). Although significant numbers of moa bones have been recovered from the dunes of the southern Hawkes Bay-Wairarapa Coast none are referable to *A. didiformis*.

In the South Island its bones are common in caves from lowland areas to about 1000 m a.s.l. in areas that receive more than 1200 mm of rain per annum. In northwest Nelson *A. didiformis* is the most common moa species in the following sites: Rua ruru Cave (760 m a.s.l.), Barron's Flat, Upper Takaka (Worthy unpubl. data); Fissures near the Magnesite Quarry Cobb Valley, 900 m a.s.l. (collection of Dorothy Cooper—December 1984); the caves of Canaan (Takaka Hill) c. 700 m a.s.l. (Worthy unpubl. data and Canterbury Museum catalogues); caves on the Salisbury Tablelands, 1000 m a.s.l., but there are also significant numbers of *Megalapteryx didinus* in these sites, (Worthy unpubl. data from Auckland Museum collection; Archey 1941); Aorere Caves, 210 m a.s.l., (Fleming 1959); Burnt Bush Cave, Aorere Valley, 300 m a.s.l., (Worthy unpubl. data); caves of the Kaihoka District, west of Whanganui Inlet 100–200 m a.s.l. (Smith 1964).

Studies in Honeycomb Hill Cave enabled Worthy & Mildenhall (1989) to show that this species became a component of the fauna of the adjacent area only when the Holocene vegetation of mixed podocarps and beech replaced the colder climate flora of a relatively open shrubland at the forest shrubland interface.

In Southland, *A. didiformis* is very rare in the coastal dune deposits (unpubl. data derived from Southland Museum collections), is similarly rare in nearby swamp deposits, e.g., Hamilton's Farm at Winton (Appendix 2), but dominates the fauna of cave deposits from nearby limestone areas, e.g., Forest Hill. At Castle Rocks, near Lumsden, Hamilton (1893) found several moas, of which all I have observed are *A. didiformis*. It was not found in caves on Mt Luxmore that are now above the bushline (Worthy 1986), but co-dominates the Holocene fauna in the nearby Te Ana-au or Aurora Cave (Worthy 1985, 1989c) with *Megalapteryx didinus*.

In Otago, *A. didiformis* remains are rare but dominate the fauna of the small "Station Deposit" sample of late Holocene age from within the Clutha River Gorge near Cromwell (Ritchie 1982). It is generally very rare or absent in all the swamp deposits of Otago and Canterbury (see Appendices 1 and 2). *A. didiformis* is not known from loess deposits.

ARCHAEOLOGICAL SITES. *A. didiformis* was rare in the large coastal moa hunter site at Houhora (Scarlett 1974) and was absent from similar sites in the Coromandel Peninsula (Davidson 1979). In the coastal sites of south Taranaki-Kaupokonui and Opua, (Appendix 4) its remains account for about 18% of the moa individuals present. This species is more abundant (30%) in the Foxton moa hunter site (Appendix 4) but a virtual absence of tarsometatarsi suggests that this species was killed elsewhere and partially butchered carcasses transported to this site. It dominated the fauna at Paremata near Wellington (Davidson 1978; Scarlett 1974; Appendix 4) and was present at other sites in the area, e.g., Te Ika a Maru (Davidson 1976) and Makara Beach (Yaldwyn 1959). In the South Island in areas around and west of Nelson, although the sites are small, *A. didiformis* is the most common moa represented (Wilkes et al. 1963; Millar 1964, 1967; Wilkes & Scarlett 1967).

In eastern districts of Canterbury, Otago, and Southland it is usually very rare (Scarlett 1974; Anderson 1989), but significant numbers were found at Papatowai (Teviotdale 1937, 1938; Scarlett 1974). It was recorded at Owens Ferry near Arrowtown, in an archaeological site, by Ritchie & Harrison (1981) and from Hawksburn (Anderson 1983b).

The distribution and relative abundance of *A. didiformis* in natural and archaeological sites show that this moa was primarily a lowland-hill country species.

Megalapteryx didinus (Owen)—Upland moa

NATURAL DEPOSITS. *M. didinus* is a South Island endemic with no validated North Island records (Worthy 1989d). It ranged over the length of the South Island but was markedly local in distribution. In the great swamp deposits of Canterbury for example, it was rare at Kapua and Glenmark (Scarlett 1969; Appendix 1) or absent (Pyramid Valley). It was absent from the dune deposits of Southland. Yet inland it is the most common species represented among the isolated finds of Central Otago such as Cromwell, Old Man Range, Manuherikia, Lake Wakatipu, Queenstown, and Kingston as listed by Oliver (1949: 152–155). Large Holocene deposits of bones of this species are known only from the subalpine zone in Takahe Valley, Mt Owen, and Mt Arthur (Worthy 1989c). Its bones are also common in caves in western areas, particularly at the Honeycomb Hill Cave near Karamea. However, there the deposit in which this species was most abundant (The Graveyard) was deposited during the Otira Glaciation when the area was at the upper montane forest-subalpine shrubland interface zone (Worthy & Mildenhall 1989). Yet it persisted there into the Holocene, co-existing with the Little bush moa (*A. didiformis*). In the Holocene sites on Mt Owen and Mt Arthur *M. didinus* is numerically the dominant species and in the Takahe Valley sites it was the only species. Below Takahe Valley the Tunnel Burn flows through Aurora Cave and there equal numbers of *M. didinus* and *A. didiformis* occur (Worthy 1989c). Radiocarbon dates for bones of *M. didinus* show that it was present in the Oparara Valley during the Otira Glaciation and into the early Holocene Worthy (1988b). Dates of 11 850 ± 2250 yr BP and 3350 ± 70 yr BP have been obtained for bones from Mt Owen (Worthy 1989 b) and 646 ± 95 yr BP for a specimen from the Cromwell area (Rich et al. unpubl. data).

ARCHAEOLOGICAL SITES. *M. didinus* is rare in archaeological sites which are mainly lowland in distribution. However it was present, although rare, at Papatowai (Teviotdale 1938; Scarlett 1974), Pounawea (Scarlett 1974), Woolshed Flat-Aviemore (Trotter 1966, 1967), Hawksburn (Anderson 1983b), and Rotokura at Cable Bay near Nelson (Scarlett 1974).

SUMMARY. *M. didinus* was primarily an upland species preferring the relatively open habitat of the upper montane forest and the very open herb and tussocklands of the subalpine zone.

Pachyornis mappini Archey —Mappin's moa

NATURAL DEPOSITS. *P. mappini* was confined to the North Island. The oldest occurrence is in a swamp deposit of Otira Glacial age at Tangatupura (Worthy 1987) and was there very common, occurring in roughly equal proportion to *Euryapteryx curtus* with a single *Dinornis struthoides*. In the King Country, *P. mappini* was not common (Millener 1981), accounting only for a small proportion of the total. As stated earlier the numerous cave sites found there are presumed to be predominantly Holocene in age. In the dune lands of late Holocene age in the far north *P. mappini* was present, but was rare in comparison with *E. curtus*. In other Holocene sites it was, however, relatively common: two swamp sites near Wanganui (Makirikiri and Riverlands), (Worthy 1989d) contained significant numbers of bones of this species, and it dominated the fauna at Poukawa in Hawkes Bay (Appendix 3).

The data may be interpreted as follows: in dunes and cave deposits *P. mappini* is rare but in some swamp sites it is comparatively common.

ARCHAEOLOGICAL SITES. Rowland (1977) listed bone material from Tairua, Coromandel, which suggests that six of nine moa individuals were *P. mappini*. However, the species is generally only common in sites around south Taranaki, e.g., Opua (Fyfe 1988, but note my re-analysis Appendix 4), Kaupokonui (Buist 1963; Foley 1980) (Appendix 4), Ohawe, or Waingongoro (Buist 1960; Buist & Yaldwyn 1960). Early records, for example, Buist (1963), in which *P. mappini* is reported as the predominant species are misleading because bones of this species were incorrectly differentiated from those of *E. curtus*. It is common in the Foxton moa hunter site (N148/1) (Appendix 4) but the virtual absence of tarsometatarsi, compared with femora and tibiotarsi, suggest that the species was killed some distance away and partially butchered carcasses transported to the site.

SUMMARY. The distribution of the species in natural deposits and of the archaeological sites in which it is common suggest that the species was primarily lowland and probably preferred the productive forest edge or shrubland ecotones provided by wetlands.

Pachyornis elephantopus (Owen)—Heavy-footed moa

NATURAL SITES. This relatively uncommon species is restricted to the South Island (Worthy 1987, 1988a). In northern areas it has been found near Takaka and in Honeycomb Hill Cave, but all are Otira Glacial in origin (Worthy & Mildenhall 1989; Worthy unpubl. data). It is present, but rare, in undated deposits around Punakaiki, e.g., Metro Cave (Millener 1980), and absent from subalpine sites. It is most common in lowland swamp sites of Holocene age, in eastern areas, e.g., Pyramid Valley, Albury Park, Kapua, Enfield, and Glenmark (Scarlett 1969; Appendices 1 and 2). Only in O'Malley's Swamp, Paerau, Central Otago, does it dominate the fauna. It is present in in eastern loess deposits as evidenced by the following specimens in the Canterbury Museum: CM Av 9620, Av 25568, Av 26753, CM Unreg - Birdlings Flat, and was present, albeit rarely, in the Southland dunes (Worthy 1989a).

ARCHAEOLOGICAL SITES. Leg bones of *P. elephantopus* are of similar size and robustness to those of *Euryapteryx geranoides* and as a result it is very difficult to distinguish one species from the other using only these bones, particularly if they are in the fragmentary state so common in archaeological contexts. This has resulted in many misidentifications. However it has been recorded from Redcliffs near Sumner, Papatowai, Pounawea, Hawksburn, Tai Rua, Shag River, Waimataitai Mouth, and Waitaki River by Scarlett (1974), to which Anderson (1983b) adds Rakaia, Awamoa, Tautuka Point, Port Craig, Gooseneck Bank, Woolshed Flat, and Luggate. This shows primarily an eastern and southern distribution. There are, however, relatively more sites in the Otago region. In archaeological sites *P. elephantopus* is never the dominant species (see Scarlett 1974), although my observations of the Papatowai collection at Otago Museum show that smaller individuals of this species were misidentified as *Eugapteryx*, thereby underestimating the true representation of *P. elephantopus*.

SUMMARY. *P. elephantopus* inhabited mainly eastern lowlands during the Holocene and ranged into the west only during the Otira Glaciation.

Pachyornis australis Oliver—Crested moa

NATURAL SITES. As this species has only recently been validated and its postcranial skeleton described (Worthy 1989a), it is as yet recognised from few sites. It is known from only the South Island, where it was common in the Otira Glacial fauna at Honeycomb Hill Cave (Worthy & Mildenhall 1989). In Holocene sites it is known from subalpine sites in Mt Owen and montane sites on Salisbury Tableland, near Mt Arthur (Worthy 1989a, 1989c), Barrons Flat upper Takaka, and Takaka Hill (Worthy unpubl. data), from near Inangahua, and from the Southland dunes (Worthy 1989a).

ARCHAEOLOGICAL SITES. *P. australis* is not yet recorded from any archaeological site. The limited data available for *P. australis* suggests that it preferred mainly western montane and subalpine regions.

Emeus crassus (Owen)—Eastern moa

NATURAL SITES. *E. crassus* is a South Island endemic. The large Otira Glacial and Holocene samples of Honeycomb Hill Cave do not include this species. Other than unconfirmed records from Metro Cave, near Punakaiki (Millener 1980), and the Kaihoka lakes district (Smith 1964), it is absent from the west, e.g., west of Nelson, the Buller area, and the West Coast. It is very common, in fact often the most abundant species, in Holocene swamp deposits of Canterbury and Otago (Appendices 1 and 2) and it is the dominant species among the collections from the Southland dunes, e.g., Riverton, Colac Bay, Wakapatu, and Greenhills (unpubl. data from the Southland Museum Collection). Hamel (1977) found that the distribution of *E. crassus* was significantly biased toward coastal areas in the Otago-Southland region. It is present in silts of the Hillgrove Formation and in the overlying loess deposits at the Shirley Stream site, Cape Wanbrow (Grant-Mackie & Scarlett 1973; pers. observ.). Bones of Otira Glacial age were collected and dated from this site by Burrows et al. (1981).

ARCHAEOLOGICAL SITES. *E. crassus* is absent from archaeological sites in the Nelson-Takaka area and dominates the Marfell Beach-Lake Grassmere fauna in Marlborough (Scarlett 1974). In Canterbury, Scarlett (1974) records *Euryapteryx geranoides* as the most common species at Redcliffs-Sumner (53%), with *Emeus crassus* being the next most abundant (41%) and together accounting for 94% of the fauna. The large excavations directed by Haast in 1872 at this site revealed a huge number of bones tabulated by Haast (1875). At this time considerable confusion existed concerning the taxonomy of moas. Bones now attributable to *Emeus* were called *Meionornis casuarinus*, *M. didiformis*, and *E. rheides* by Haast and what we now describe as *E. geranoides* he termed *Dinornis crassus* and *Euryapteryx gravis*.

Although Haast did not determine minimum numbers of individuals present he did list numbers of bones for each taxon. Translated into the modern taxonomy Haast thus recorded 214 bones of *Emeus*, and 53 bones of *Euryapteryx*. Since Haast's taxonomy was almost entirely based on measurement and we now know that the upper size range of *Emeus crassus* and lower size ranges of *Euryapteryx geranoides* overlap, the disparity probably is not as marked as it appears. Still these data do suggest that at Redcliffs *Emeus* may have been more common than *Euryapteryx*.

At the middens at the Rakaia River mouth Haast (1872) reported *Emeus crassus* (then called *D. didiformis* and *D. casuarinus*) to be the most numerous. *Euryapteryx geranoides* (called by Haast *D. crassus*) was the second most abundant species. Haast (1872) recognised that the relative proportions of bones of each species in the cultural site at Rakaia were basically similar to that in the natural Glenmark site.

> "During the examination of the kitchen middens... I was at once struck by the curious fact that the more or less frequent presence of bones coincided closely with similar observations made concerning the skeletons imbedded in the Glenmark swamp, and which showed that the frequency of the different species in that locality was not accidental."

Trotter (1972) contended that the only moa present in his excavations of the Rakaia site was *E. geranoides*. However, the bone material Trotter recovered was mainly fragmented leg bones (310 pieces weighing 1762 gm, and 13 pieces weighing 29 gm). Scarlett, who identified Trotter's bone material, admits that it is very difficult to distinguish leg bones, especially tibiotarsi, of *E. crassus* from those of *E. geranoides* (Scarlett 1974). With this I agree and further maintain that since their size range overlaps, it is impossible to distinguish these species from the majority of fragments likely to come from leg bones. Thus, I believe the identifications of the bone as *E. geranoides* by Trotter and Scarlett reflects their expectations: ".... identified as *Euryapteryx gravis* is not surprising in itself; it is by far the most common species to be identified from South Island moa-hunter sites." (Trotter 1972).

At Waimataitai *E. crassus* was "the predominant moa" (Trotter 1965), but at Papatowai the abundance of *Emeus* is less than half that of *E. geranoides* although it was still very common (Teviotdale 1938; Scarlett 1974). In the following sites although generally few bones are represented *Emeus* bones are either the most common or in equal abundance with those of *E. geranoides*; False Island, Kaka Point, Little Papanui, Andersons Landing, Long Beach, and Seacliff (Scarlett 1974). For the large sites of Shag River and Waitaki River *E. geranoides* is cited by Scarlett to be the most abundant, but bones on which these observations are based were largely derived from excavations either in the nineteenth century (Shag River) or 1930's (Waitaki River; (Teviotdale 1939). A recent excavation at Shag River suggests that bones *Emeus* are more abundant than previously recorded (pers. observ.). It is probable that their smaller size resulted in a bias during early excavations towards recovery of the larger bones of *E. geranoides*. The large in-land moa butchery site at Hawksburn was dominated by bones of *E. geranoides* (Anderson 1983c).

Scarlett (1974) reported *Euryapteryx* n. sp. to be abundant at the Old Neck site on Stewart Island. However, because all bones in Otago Museum labelled in Scarlett's handwriting as *Euryapteryx* n. sp. from Papatowai and Pounawea are *Emeus* (pers. observ.) then I predict that the Old Neck bones will also prove to be *Emeus*, thereby showing that *Emeus* was on Stewart I. This also means that the representation of *Emeus* at Papatowai had been underestimated in previous accounts.

SUMMARY. *E. crassus* had primarily a lowland eastern distribution in the South Island during the Holocene, but also occurred on Stewart Island.

Euryapteryx geranoides (Owen)—Stout-legged moa

NATURAL SITES. *Euryapteryx geranoides* was distributed throughout New Zealand from North Cape to Stewart Island in lowland areas. However there are marked patterns in its distribution: it was rare in the North Island in all areas except the coastal dune areas of the south eastern region from Hawkes Bay to the Wairarapa. It is virtually the only moa species recorded from this area (Oliver 1949; Brodie 1950; Yaldwyn 1966) although rare records of its small congener *E. curtus* do occur. Hutton (1906) recorded *Emeus crassus* from Castlepoint but this was transferred to *Euryapteryx* by Oliver (1930) as the holotype of *E. kuranui*. Archey (1941) reduced it to synonymy with *E. gravis*, and *E. gravis* was reduced to synonymy with *E. geranoides* by Cracraft (1976). Worthy (1988a) considers that the size variation in *E. geranoides* is clinal but a temporal relationship is now also being examined.

In the South Island, *E. geranoides* is very rare in western districts: Millener (1980) and Anderson (1989) reported records, that I have not confirmed, of this species from Metro caves and other caves in the Punakaiki area; Archey (1941) and Oliver (1949) record it from Salisbury Tableland, Mt Arthur (AIM), but I believe the specimens (AIM Moa 18.1 = 116) are more correctly identified as *Pachyornis australis*. I have found only one specimen, of Otira Glacial age, in the extensive deposits at Honeycomb Hill Cave. Parts of one individual occur in Ngarua Cave Takaka Hill and rare additional specimens are known from nearby caves (Worthy unpubl. data). In contrast, in eastern areas it is common (see Appendices 1 and 2), appearing, from these data, to be relatively more numerous in the swamps of South Canterbury and North Otago, such as at Hamiltons and Herbert, than those in north Canterbury. In most natural sites it is less abundant than *E. crassus*.

Bones of *E. geranoides* have been recovered from the coastal dunes at Riverton in Southland (Oliver 1949) and also from Stewart Island (Benham 1910).

It is absent from subalpine sites, previous records for such areas being now referred to *P. australis* (Worthy 1989a).

ARCHAEOLOGICAL SITES. Mirroring its "natural" distribution *E. geranoides* is rare or absent from most North Island archaeological sites (Scarlett 1974). Leach (1979) reported *E. geranoides* and *E. gravis* (identification by R. J. Scarlett) which are here regarded as smaller and larger specimens of one species from coastal sites in the southern Wairarapa. But because *E. gravis* was considered to be a South Island species, and because the bone pieces were small, Leach considered that the bones had been obtained by trade and were not local in origin. However, since *E. geranoides* was the dominant moa in natural deposits in this area, and since its size range here overlapped that of bones from South Island sites, it is probable the bones were from locally killed moas. However, as the band of dune country is narrow the moa population was probably small and therefore was exterminated quickly, resulting in greater use being made by the Maori population of the few bones available.

In the South Island *E. geranoides* is found only in Marlborough, Canterbury, and Southland-Otago (Scarlett 1974). It was the dominant species at the Wairau Bar site (Falla 1941), arguably so at Redcliffs (see discussion under *Emeus* above), but definitely so at Papatowai, Pounawea, Hawksburn, Shag River, and the Waitaki River mouth (Scarlett 1974). Scarlett recorded it from 27 South Island sites, concluding it to be the dominant species occurring in South Island middens. In a recent visit to Otago Museum I checked the identifications of many Papatowai bones and observed the following: many bones are labelled as "*Euryapteryx gravipes*", a synonym of *E. geranoides*, byut all are referrable to *Pachyornis elephantopus* (small and of size range); all bones referred to as *Euryapteryx* n. sp. are small *Emeus crassus*. From a sample of 125 complete bones *Emeus*, *Euryapteryx*, and *Pachyornis* I determined the MNI as follows: *E. geranoides* 21, *E. crassus* 11, *P. elephantopus* 7. Thus, Scarlett (1974) underestimated the frequency of *Pachyornis* and *Emeus*, and overestimated the frequency of *Euryapteryx*. However, the data can be reinterpreted as follows: there are only 14 sites where more than one bird of either *E. geranoides* or *E. crassus* are represented. *E. geranoides* is the dominant moa at eight of these sites, five of which are in the southern region, and *E. crassus* dominates in three sites. In three sites the frequency of occurrence of *E. geranoides* is not significantly different from that of *E. crassus*. Bones of *E. geranoides* are bigger and more durable than those of *E. crassus* and dominate archaeological sites only in the eastern South Island particularly in the Marlborough and Otago region.

SUMMARY. The archaeological and natural distribution of *E. geranoides* match each other surprisingly well. The species had a New Zealand wide distribution in the lowlands, but was a significant component of the avifauna in only eastern areas. In the South Island it was relatively most numerous in the Otago-Southland region, and at the Wairau Bar site.

Euryapteryx curtus (Owen)—Coastal moa

NATURAL SITES. *Euryapteryx curtus* is a North Island endemic. The fossil fauna of the dune sites of the far north, including areas near Cape Reinga, North Cape, and Houhora, was studied by Millener (1981) who found *E. curtus* dominated the moa fauna (69%). At Tokerau Beach, *E. curtus* is the most common moa species. At the small dune sites near Whangarei and Waipu available bones suggest *E. curtus* was the most abundant species. The table of measurements for a large sample of bones from Pataua River, given by Thorne (1876), strongly suggests that the main species in his collection was *E. curtus*, but the whereabouts of this collection is unknown.

I have collected this species from natural dune deposits at Harataonga Bay on Great Barrier Island. In the King Country, *E. curtus* was far less significant (15%—Millener 1981) than in the above sites. Although found widely over the rest of the North Island, it is abundant at only two other sites—Te Aute (Hamilton 1889, Appendix 3) and Tangatupura (Worthy 1987) both of which I consider to be of Otira Glacial age (Worthy 1987). Although undated, another site of possible Otira Glacial age is in Spotlight Cave in north Taranaki. Here, specimens were collected from within stream gravels and others from surface deposits beneath entrances (Medway 1968), but these different origins were not distinguished. Millener (1981: 816) listed species and their frequency from here showing that *E. curtus* accounted for 32% of the MNI of moa and *E. geranoides* 14%. This high proportion of *Euryapteryx* is totally unlike any other King Country-Taranaki site. The Spotlight Cave fauna also includes bones of the largest size range of *P. mappini* which are known only from Otira Glacial aged deposits (Worthy 1987). Gravels from Ecch Cave on the opposite side of the Mokau River to Spotlight Cave, and only about 2 km distant, also contained bones of the largest size of *P. mappini* (Worthy unpubl. data). Sedimentation in both these caves was probably contemporary and of Otiran age. *E. curtus* was not present in the Holocene swamp deposits, Makirikiri, Riverlands, and Takapau Rd in the Wanganui and Horowhenua areas (Worthy 1989d). A late Holocene site at Clevedon (Appendix 3) did, however, contain significant numbers of *E. curtus*.

ARCHAEOLOGICAL SITES. Scarlett (1974) recorded *E. curtus* (*E. exilis* included) as the predominant species at Houhora. In Coromandel sites, Davidson (1979) recorded *E. curtus* as the most frequently occurring species: it is in 6 (possibly 8) sites out of 10. In the central North Island on the Volcanic Plateau it was the only species recorded from the Tokoroa moa hunter site (Law 1973) and was present in Whakamoenga Cave-Lake Taupo (Leahy 1976). It is the most abundant species in south Taranaki sites and is a prominant species in the Foxton moa hunter site (Appendix 4).

SUMMARY. *E. curtus* was a North Island species, with a predominantly coastal distribution, a reflection of the distribution of fossiliferous sites in the areas previously containing suitable habitat for this species. Inland sites where it was numerous are probably all of glacial age except on the Volcanic Plateau.

Dinornis species

Summarising the distribution of each *Dinornis* species is more difficult than for species in other genera because *Dinornis* species are separated only by size. Previous species boundaries have been drawn at small size intervals and these were progressively amalgamated till Archey (1941) accepted six species, three in each of the North and South Islands. Oliver (1949) increased the total to eight, but Cracraft (1976) reduced the total to four. I accept only three, each represented in both the North and South Islands (Worthy 1988a, 1989d). Size frequency analyses of large samples of dinornithid bones from single sites can enable size boundaries to be defined around data clusters that distinguish three species. The problem is that the species boundaries thus revealed do not coincide with those used by Archey or Oliver, and there is also north-south clinal variation (Worthy 1989d). Therefore, unless measurements are recorded, interpretation of past records within the current species framework is difficult and may be often not reconcilable.

D. struthoides **Owen**—Slender moa

NATURAL SITES. Millener (1981) found *D. struthoides* to be the most abundant dinornithid, yet to comprise only 5% of the far north moa fauna from dune deposits. In the King Country cave assemblage it was the most common dinornithid and constituted 10% of all moas (Millener 1981). Although Millener (1981) did not record *D. struthoides* from caves of the Puketoi Range I have seen remains of six individuals in Gillespie's Folly Cave at Makuri (unpubl. data). Further south, near Martinborough, it was the dominant dinornithid with 12.5% of the moa minimum number of individuals (MNI) (calculated from data in Millener 1981). It was present in the Te Aute swamp deposits (Hamilton 1889; Appendix 3) and at Poukawa it was the dominant dinornithid (7.4% MNI of all moa). In the swamp sites of Makirikiri, Riverlands, and Takapau Road (Worthy 1989d), *D. struthoides* represented 7.1%, 9.6%, and 25% of the MNI of moa, respectively. In the South Island, *D. struthoides* is present but is relatively rare in subalpine sites, e.g., on Mt Owen. It is rare also in northwest Nelson (some specimens previously assigned by Oliver (1949) to *D. torosus* from Takaka, I include in *D. novaezealandiae*; Worthy 1989d), but has been found in Honeycomb Hill Cave and cave deposits in Buller Gorge. It is known also from a number of South Island swamp deposits (Appendices 1 and 2) where it generally outnumbers other dinornithids, the principal exception being Pyramid Valley. It is unknown from loess deposits.

ARCHAEOLOGICAL SITES. Scarlett (1974) records *D. struthoides* (inclusive of *D. gazella*) from Houhora (3.5% of moa bones but the most common dinornithid), a number of sites on the Coromandel peninsula, Kaupokonui in south Taranaki, and sites in the Wellington region in the North Island. Of the collections I examined (Appendix 4) I could only confirm its presence in Paremata, near Wellington. There are few South Island sites: Rotokura at Cable Bay, Awamoa, Papatowai, King's Rock, Shag mouth, Seacliff, Tautuku north, Hawksburn, and the Waitaki River mouth (Scarlett 1974; Anderson 1983b).

SUMMARY. *D. struthoides* had a wide distribution in both the North and South Islands ranging from lowlands to subalpine areas. In the North Island it is usually the most abundant dinornithid and is relatively more abundant in inland cave sites than coastal dune sites. However, at Makirikiri, near Wanganui, where *D. novaezealandiae* is more frequent. It is comparatively rare in the South Island but is widespread. The distribution of this species shows no correlation with particular altitude or rainfall zones.

D. novaezealandiae **Owen**—Large bush moa

NATURAL SITES. *D. novaezealandiae* was very rare in the far north dune sites but was relatively common (7.1% MNI of moas) in the King Country cave assemblage (Millener 1981). In caves at Waikaremoana and Coonoor it was the most common dinornithid with 19.2% and 19.0% MNI of moa respectively (calculated from data in Millener 1981). In caves near Martinborough it represented 7.1% MNI of moa and was less common than *D. struthoides*. In swamp deposits it was absent from Clevedon (South Auckland—Millener 1981: 800), apparently rare at Poukawa, and absent from Tangatupura (Worthy 1987). At Te Aute the picture is confusing, but the survival of specimens in the National Museum of New Zealand (NMNZ) and Canterbury Museum suggests *D. novaezealandiae* to have been less common than *D. struthoides* and *D. giganteus* (Appendix 3). Measurements of the entire original collection from Te Aute, made by James Park, are preserved in his original report to Hamilton in the NMNZ Hamilton file. Reinterpreted in light of synonymy and presently accepted species sizes (Worthy 1989d) a different proportion of species emerges. Bones of *D. novaezealandiae* are the most common, those of *D. giganteus* the next most common, and those of *D. struthoides* the least common. At Makirikiri, near Wanganui, it was the most common dinornithid and second most abundant moa representing 16.6% MNI (Appendix 3). At Riverlands and Takapau Road (see Worthy 1989d) the frequency of *D. novaezealandiae* was 7.7% and 21.9% respectively, a similar abundance to that of *D. struthoides*.

In the South Island, *D. novaezealandiae* equates with *D. robustus* and, in part, *D. torosus*, of Oliver (1949) and is the most common dinornithid in western districts, including Punakaiki, Buller, Karamea, and Takaka. In these areas of the West Coast and northwest Nelson the maximum size that individuals attained is less than that for North Island districts, and the smallest individuals, although of the same size as the smallest at Makirikiri, were called *D. torosus* (Worthy 1989d). It has been recorded from

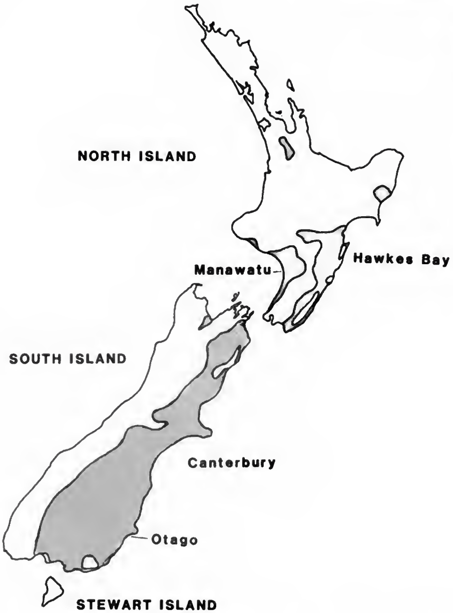


Fig. 2 A map of New Zealand showing those areas receiving less than 1200 mm rain per annum (shaded) after Tomlinson (1976).

a subalpine site on Mt Owen (2 individuals) by Bell & Bell (1971) and from a number of lowland swamp sites (Appendices 1 and 2), but in the latter it is usually rare.

ARCHAEOLOGICAL SITES. *D. novaezealandiae* is rare in most archaeological sites but is recorded from Tairua and Whiritoa on Coromandel Peninsula, Ohawe (= Waingongoro) in Taranaki, and Paremata near Wellington by Scarlett (1974). I could not confirm its presence in Taranaki sites, but did identify it from the Foxton site (Appendix 4). The bone of *D. hercules* from Makara Beach (Scarlett 1974) I reidentified after inspection of measurements and photographs in the NMNZ as *D. novaezealandiae*. In the South Island (referred to as *D. robustus*) Scarlett (1974) lists the following sites in which it is found: Greville Harbour on D'Urville Island, Papatowai, King's Rock, Tautuku, Seacliff, and Shag River. Anderson (1983b) lists rare occurrences in four more sites.

SUMMARY. *D. novaezealandiae* was found throughout New Zealand but was rare in coastal dune sites and in the eastern South Island. Only in the inland cave areas of the North Island, Makirikiri, and western districts of the South Island was it relatively common in the Holocene.

D. giganteus Owen—Giant moa

NATURAL SITES. *D. giganteus* is generally rare in North Island fossil assemblages: 1.1% MNI of moas in the dunes of the far north, and in caves; 3.6% in the King Country, 1% at Waikaremoana, 2.4% at Coonoor, and 1.8% at Martinborough (data from Millener 1981). It was present at Te Aute (but of unknown relative abundance) and rare at Makirikiri (3.4% MNI of moas), but more frequent at Takapau Rd; 12.5% (Worthy 1989d). It was rare at Poukawa (Appendix 3). In the South Island it is not present in the Honeycomb Hill Cave assemblages. It is very rare or absent from all western or northwestern sites and is only present in eastern swamps (Appendices 1 and 2). Even in these sites it is relatively rare, except at Pyramid Valley. Its huge size is so impressive that far more numerous remains of smaller species seemingly pale into insignificance beside them.

ARCHAEOLOGICAL SITES. Considering its relative rarity in natural sites it is recorded from a surprisingly large number of North Island archaeological sites. Scarlett (1974) lists Houhora, several Coromandel and Taranaki sites, and Paremata near Wellington (see Appendix 4).

The South Island sites listed include: Redcliffs, Papatowai, Pounawea, Little Papanui, Andersons Landing, and Shag River. Anderson (1983b) lists a further six sites, all from eastern areas.

SUMMARY. *D. giganteus* was rare throughout the North Island. In the South it seems to have been confined to eastern lowland regions but even there was usually the rarest moa. The data in (Appendix 4), indicates that although *D. giganteus* is often present it is one of the least common species in terms of MNI.

New Zealand climate during the Holocene

The start of the Holocene about 10 000 years ago was marked by a rapid climatic amelioration in which the Late Glacial shrubland-grasslands of the South Island were replaced by widespread tall forests. The North Island had been largely forested since 14 000 BP. Mean annual temperatures were c. 4.5°C greater than those of the Otira Glacial. Since then the climate has remained essentially mild supporting widespread tall forest. However, minor perturbations are summarised by McGlone (1988): The period 10 000 to 7000 BP was the "mildest, least seasonal, perhaps warmest time". Around 7000 BP the climate began to cool and the incidence of wind, drought and frost probably increased. This resulted in changed compositions of some forests but otherwise did not markedly affect lowland areas (see vegetation section). Present conditions were probably achieved about 2000 BP.

The map of rainfall zones (Fig. 2) portrays a pattern that has probably been relatively constant throughout the Holocene mainly because of the topographical effect of the major mountain chains. This shows that all of the western South Island and most of the North Island receives over 1200 mm rain per annum. In the North Island rainfall is between 800 and 1200 mm in South Taranaki, Manawatu and east of the main ranges south of Napier. In the South Island virtually all eastern areas receive less than 1200 mm. It is especially dry in Marlborough, Canterbury, and Otago with some areas of central Otago receiving less than 400 mm.

General vegetation reconstruction for the Holocene

I restrict my assessment of vegetation to the Holocene because most fossil and all archaeological deposits pertain to this period. The few Otira Glacial deposits will be considered in the next section. Reconstruction of the vegetation will be aimed at those areas or regions where most fossil data are from, and areas for which there are no fossil data will not be specifically considered. General patterns here are as described by McGlone (1988) unless otherwise stated. I will not review the literature leading to a synopsis of the vegetation cover of New Zealand in the Holocene. This has been done by McGlone (1980, 1983, 1985, 1988).

By 9500 BP rimu (*Dacrydium cupressinum*) was the dominant tall podocarp in forests in all but dry south-eastern districts of the North Island. By this time South Island eastern lowlands had tall matai-(*Prumnopitys taxifolia*)-totara-(*Podocarpus totara*)-kahikatea (*Dacrycarpus dacrydioides*) dominated forests. Western areas predominantly had a rimu-southern rata-(*Metrosideros umbellata*)-kamahi (*Weinmannia racemosa*) association. Inland and upland districts had shrublands similar in structure to those of the Late Glacial. With the slight cooling of climate around 7000 BP expansion of beech commenced and by 2500 BP the modern distribution was largely achieved. The fertile lowlands on the drier eastern side of the South Island were in tall to low podocarp-broadleaf forest. And

> "... inland, the driest regions of the central Otago McKenzie Country were abruptly covered with a low forest, primarily of mountain toatoa, bog pine, mountain totara, kanuka and, at higher altitudes, silver beech. This dry, inland, low forest extended from central Otago northwards through north Otago-South Canterbury districts, under the shadow of the highest part of the Southern Alps and into the drier regions of north Canterbury and Marlborough." (McGlone 1988: 103).

Between 2500 and 1500 BP much of these dry inland forests were destroyed by natural fire. In the lowland forests of western North Island the pollen record suggests that the predominance of "Rimu gave ground to matai, totara and a host of broadleaved species. Climbing vines and treeferns became markedly less common, while hutu, which favoured mild, moist conditions, faded to near extinction over large areas of the North Island..... These changes continued in lowland forests until at least 2000 years ago. Most of them can be related to the disturbance caused by increased winds droughts and frosts." (McGlone 1988: 103).

In short these lowland North Island forests were wetter and denser before 2500 BP than they are now, where they still exist. McGlone (1988:104) continues:

> "About 1500 years ago.... Only 10 percent of the total land area lay above the alpine tree line. In southeastern South Island, extensive dry grasslands occupied central Otago and parts of surrounding districts. Treeless grasslands were common in the basins of the Southern Alps, the isolated frost hollows of the North Island, and on river beds and sand dunes throughout. However, even in predominantly grassed regions, shrubs were common, and patches of forest survived even in the most extensively burnt regions. Drier regions with poorer soils—such as part of the Canterbury Plains—appear to have had low forests of kanuka. Wherever the landscape was disturbed frequently—such as on sites close to rivers,....—shrublands, low forests and regenerating forest were common."

The extensive deforestation that occurred in the last millenium is extensively reviewed by McGlone (1983). Species ranges during the period of their extirpation can only have shrunk, therefore the vegetation conditions occurring immediately before human arrival are those that are most relevant in habitat reconstruction.

More specific vegetation reconstruction

Eastern South Island. For some of the areas from which moa fossils are derived, local vegetation reconstructions are available. Moar & Mildenhall (1988) report pollen spectra from coastal sites in Canterbury that reveal a history of swamp forests in these areas over much of the Holocene. At Timaru, a shrubland or low forest was present 6730 BP (Moar 1971). Moar (1970) documents the vegetation history of the area around the Pyramid Valley site and concludes that "the slopes surrounding the swamp seem to have been clothed by a mosaic of forest and shrubland... that... persisted throughout the history of the deposit" and thus during the period of moa entrapment. In summary, much of coastal Canterbury had extensive swamp forests dominated by podocarps. But there were areas interspersed among these forests and on most of the Canterbury Plains where the ground was drained and therefore drier. These areas supported shrubland and low forest communities. An example of such low forest-shrubland community may be preserved by Eyrewell Scientific Reserve on the North side of the Waimakariri River (Molloy & Ives 1972). Charcoals in the soil of adjacent areas show that a kanuka (*Kunzea ericoides*) community existed there about 1000 years ago. The present low forest is "dominated physiognomically by slender trees of kanuka up to 18 cm in diameter and 6–7 m tall, forming an irregular and branched canopy.... A shrub tier about one metre tall is usually present... " (Molloy & Ives 1972: 686). Where the tree canopy is discontinuous a shrubland of kanuka trees, scattered shrubs of kanuka, manuka, (*L. scoparium*), broom spp., (*Carmichaelia* spp. and *Coprosma* spp and some grasses occur. The overall vegetation structure would have been an intricate mosaic of forest and shrubland relatively more open in structure than the wet western podocarp forests. The numerous wide braided rivers would have contributed to this open mosaic by providing extensive forest margins. The inland areas of Canterbury or Otago also supported mosaics of forest and shrubland, but for much of the Holocene the driest areas of Otago had extensive grasslands.

North Westland/northwest Nelson. Throughout the Holocene a wet dense podocarp-broadleaved forest dominated by rimu prevailed over most of the region where fossil moa are found, i.e., Punakaiki, Karamea, Patarau. At present towards higher altitudes beech progressively replaces podocarps. In the Oparara Valley the forest is very wet with moss covering the forest floor and tree trunks. On Barron's Flat (750 m a.s.l) the podocarp-beech forest is very dry with no moss. By 900 m, for example, Salisbury Tableland or Takaka Hill, the vegetation is predominantly silver beech. The absence of extensive moss carpets on Takaka Hill reflects the regular dry periods experienced there.

Subalpine areas. There has been little alteration of the area in subalpine vegetation during the Holocene. Montane forests grades into grassland; sometimes beech forest grades directly to tussock, at other places a shrubland of variable width, typically with *Olearia*, *Dracophyllum*, and *Hebe* species, forms an intermediate zone.

North Island—south east coastal dune region. The narrow belt (about 100 m wide) of coastal dunes probably supported a shrubland vegetation (as did the sites in the far north) during accumulation of the fossils. Tall forests and wetlands formed their inland boundaries.

Coastal south Taranaki and Manawatu. The south Taranaki coast is backed by a duneland zone up to a few kilometres wide. Formation and movement of these dunes has resulted in numerous small wetlands. This zone of dunelands widens markedly south of Wanganui and is most extensive between the Rangitikei and Manawatu Rivers. The whole of this area receives a relatively low rainfall 800–1200 mm. The data presented by Shepherd (1987) and C. M. Lees (in Shepherd 1987) suggest that during the latter part of the Holocene the Rangitikei/Manawatu dunelands would have been characterised by swamps interspersed with dunes. The dune ridges had kanuka, akeake (*Dodonaea viscosa*), matai (*Prumnopitys taxifolia*), titoki (*Alectryon excelsis*), maire (*Nestegis montana*). The swamps were dominated by kahikatea (*Dacrycarpus dacrydioides*) and pukatea (*Laurelia novaezelandiae*). Thus, a mosaic of shrubland/wetland/dense forest would have prevailed. Bussell (1988) presented data for mid and late Holocene vegetation near Waverley in south Taranaki. The late Holocene site Bussell studied was Lake Waiau; it is situated on the inland edge of the dunes, and the pollen record suggests that nearby vegetation was predominantly lowland podocarp-hardwood forest for this period. However, the presence of— in particular— manuka, kanuka, and akeake, suggests to me the presence of nearby scrub or shrubland. The combined data from Bussell's Waverley Beach site and Lake Waiau suggests to me that the coastal area had a late Holocene history of moving dunes that resulted in the formation of wetlands that were in turn eventually overrun by dunes. It seems to me likely that the dunelands provided a mosaic of forest, shrublands, active dunes, and wetlands and that inland of this were the continuous lowland podocarp-hardwood forests.

Limestone Cave Areas—King Country, central southern North Island, Waikaremoana. This area is characterised by a high rainfall, generally over 1600 mm. All the available evidence suggests that a wet, dense, tall popocarp-broadleafed forest prevailed in these areas throughout the Holocene (Millener 1981; Worthy 1984). studies from adjacent areas support this contention (McGlone & Topping 1973; McGlone et al. 1984; Green & Lowe 1985; Newnham et al. 1989).

For example, the vegetation history of the Waikato lowlands has been determined by Newnham et al. (1989) from pollen analyses of lacustrine deposits; they afford detailed chronological resolution because of interbedded tephras. These lowlands are underlain by the Hinuera formation that, although only recently formed in the Late Glacial, was then largely unforested. Forestation proceeded rapidly from about 14 500 years ago. Matai practically dominated these forests but by 11 000 years ago rimu was the predominant species and remained so until the present. However, from 5500 years ago until now, rimu declined in importance giving way to increased frequency of matai, *Phyllocladus* spp., and kauri (*Agathis australis*). This is suggestive of a drier climate in this period, thus conforming to the synthesis of McGlone (1988). These forests were probably tall with a dense undergrowth and a deep litter layer. The present high rainfall of these areas suggests that these forests were relatively wet compared to eastern lowland areas of the South Island.

Far north dune areas. Recently, pollen analyses of cores from swamp deposits behind dunes at two sites near Cape Reinga have confirmed that the area was forested over most of the Holocene, but that "shrubland has been a prominent component of the vegetation throughout the record." (Dobson et al. 1988). It is probable that this shrubland was on the wetlands and on the unstable dunes within which the fossil fauna was deposited, and that the forests were on the older stablilised dunes or nearby stable volcanic soils.

Although there is no direct evidence, it is probable that the vegetation of dunes in the North Cape Block, near Houhora, and those backing Tokerau Beach were in similar shrubland. The presence of open country birds, such as pipit and quail (Millener 1981) within the fossil fauna supports this contention.

The dunes of Tokerau Beach probably backed into a tall closed forest as did those near Cape Reinga. Millener (1981: 281) presented a pollen analysis for a sample of peat obtained behind Tokerau Beach from which he suggested that rimu dominated the vegetation of the area during the deposition of the peat, a time probably contemporary with the nearby dune formation.

DISCUSSION

Patterns of distribution, species association, and habitat preferences

The upland-subalpine component. The upland moa (*Megalapteryx didinus*) was the principal species using this area in the South Island. From a few Holocene records but principally from the Otira Glacial fauna of Honeycomb Hill, I believe that the crested moa (*Pachyornis australis*) was the main associate in this zone. It appears to have replaced its congener *P. elephantopus* in colder, wetter areas.

The principal environmental components of the subalpine zone are cold, wet, open vegetation which can be met with in southern regions at lower altitude and thus the occurrence of *P. australis* in coastal Southland. No data are available to determine the species using this zone in the North Island, but I predict that the predominant species of the shrubland areas, i.e., *Euryapteryx curtus*, filled this habitat.

Lowland, dense wet tall forests. *Anomalopteryx didiformis* was the most abundant emeid and *D. struthoides* and *D. novaezealandiae* the two most abundant dinornithids in lowland areas of the North Island that were clothed in wet, tall podocarp forests during the Holocene. In similar South Island areas, *D. struthoides* was relatively rarer leaving *D. novaezealandiae* as the dominant dinornithid. Other emeid species were relatively rare or absent in this habitat in both islands.

North Island shrubland areas. Such areas were largely confined to the coastal dunes during the Holocene and in Northland, south Taranaki, and Manawatu. *E. curtus* was the dominant species. *P. mappini* and *D. giganteus* were virtually the only other species present but were rare. It is probable that the Volcanic Plateau in the central North Island had some shrubland in the late Holocene because shrubland is likely to occur in higher, inland colder areas, so it is no surprise to find *E. curtus* in the two moa hunter sites described from this region.

In the coastal duneland regions of south Taranaki and Manawatu and in the lakeside deposit of Poukawa, Hawkes Bay, *P. mappini* was a much more significant component of the fauna than it was in Northland. These areas characteristically have a low rainfall (800–1200 mm) and numerous small wetlands. The presence of *P. mappini* in natural swamp deposits, but absence from, or rarity in, natural dune deposits and the above distribution data suggests that this species favoured shrubland around the edge of lowland wetlands in a generally dry climate. Its abundance in Waikuku Beach dune deposits (Millener 1981) may reflect the presence of an adjacent wetland. *E. curtus* and *P. mappini* are both prominent species in the Otira Glacial faunas of Te Aute and Tangatupura, corroborating the suggestions of shrubland having been the optimal habitat for these species.

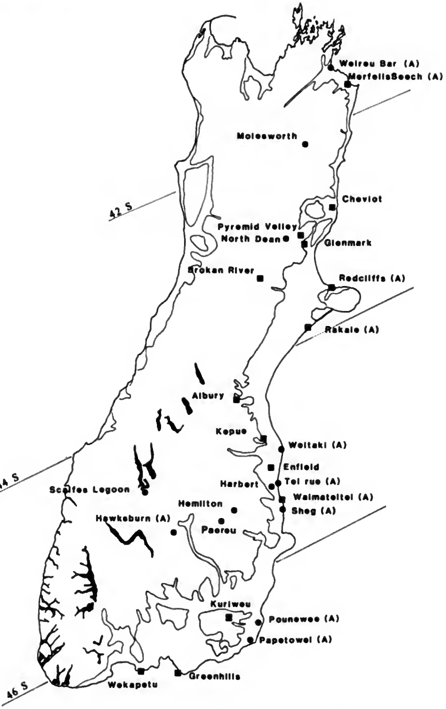
In coastal dunelands of the Wairarapa and Wellington areas *E. geranoides* replaced *E. curtus* as the predominant moa species.

South Island lowland eastern areas. During the Holocene *D. giganteus* was the dominant dinornithid and the three emeids *P. elephantopus*, *Euryapteryx geranoides*, and *Emeus crassus* were prominent members of the rest of the moa fauna. An exception is western Southland where faunas of cave deposits at Lumsden, Forest Hill, and Browns were dominated by *A. didiformis*. This area was relatively wetter than other areas east of the alps from which we have moa distribution data and was probably covered in relatively continuous dense tall forests.

The rest of the eastern lowland South Island has a dry climate. The Holocene vegetation before 1000 BP can best be described as a mosaic of vegetation types, including forest, swamp forest, low forest, shrubland, and grassland. The rivers, abundant wetlands, and vegetation mosaics resulted in a diverse array of forest margins and an often open environment. *Dinornis giganteus* was the dominant dinornithid. This general correlation of distribution and habitat type, dietary data, and its rarity in dense, wet, lowland, tall podocarp forest suggests that this species was, as has been suggested by Burrows et al. (1981), an inhabitant of relatively open forests, of forest margins, and shrublands in lowland areas. This explains its prominence in swamps and in dune deposits. This is also why it is rare in the North Island—because most fossil sites are derived from those areas previously covered in comparatively dense forests.

Fig. 3 shows those sites in which either *Emeus* or *Euryapteryx geranoides* dominate among emeids, and where there are more than 12 moas represented. Although *E. geranoides* and *E. crassus* occur together throughout the eastern zone a definite pattern emerges. *Emeus* dominates in 14 sites, of which 11 are less than 200 m a.s.l. Seven of these 11 sites are natural. In contrast, there are 13 sites where *Euryapteryx* is dominant: 6 (5 are natural) of these are found higher than 200 m a.s.l, but of the remainder, 6 are very large archaeological sites. These, like Waitaki, may be "interior focus" sites (Anderson 1989), to which transport of birds from distant hunting grounds is likely. Both species are found in dunes and loess. Their distribution, combined with the general vegetation reconstruction for those areas, suggests these species preferred relatively open vegetation with plentiful forest margins. However, Fig. 3 suggests that this habitat can be further defined. *Emeus* preferred the flat lowlands where swamp forests and wetlands were plentiful. *Euryapteryx* preferred the adjacent hill country, especially those areas which McGlone (1988) suggested supported a dry inland forest until 2500 BP. Some geographic separation of principal habitat for these two species

.3 A map of the South Island h the 200 m contour showing s in which more than 12 moa ividuals are represented and in ich either *Euryapteryx* *anoides* (●) or *Emeus crassus* is the predominant emeid. wever, O'Malley's Swamp at roa is also included, as although ninated by *P. elephantopus*, apteryx and *Emeus* occur in e numbers. Archaeological sites identified by (A), others are ural.



uld be predicted since each had relatively small zzards containing small stones and a cranial and ak structure that was relatively weak compared to at of other moas, which together suggest that both d similar food preferences. Worthy (1989e) has gued that both *Emeus* and *Euryapteryx* ate only ft vegetable matter such as leaves and fruit.

P. elephantopus occurs throughout the region d, if both frequency of entrapment in mires and presentation in middens are significant, was less mmon than *Euryapteryx* and *Emeus*. Its very ifferent beak and cranial morphology (Worthy 989e) suggest that it had a totally different diet, but r this there are no data. It is probable that it was an habitant of open forests or shrubland and forest margins and was able to utilise a more fibrous, woody vegetable diet.

The effect of habitat boundaries

Where one habitat grades into the other a mixing of faunas should occur. In Fiordland in the subalpine Takahe Valley *M. didinus* was the only species present, but immediately down slope and 300 m lower *A. didiformis* was present in equal numbers to *M. didinus*. At a lower altitude, but some distance away near Lumsden, only *A. didiformis* was present.

Other examples of this phenomenon occurs in the caves on Takaka Hill and Salisbury Tablelands where a mixture of *M. didinus* and *A. didiformis* occurs because these areas are, and have been during the Holocene, intermediate between the subalpine zone and the lowland dense wet forest zone. Similarly, in Otago *M. didinus* is mixed with *Euryapteryx geranoides* as many areas here were essentially subalpine but graded into the open dry shrublands favoured by *E. geranoides*. This mixing effect can also happen over time, for example, if a subalpine or montane habitat is transformed into a typically lowland habitat, as occurred in the Oparara (Worthy & Mildenhall 1989).

Correlation of some morphological characters with proposed ecological preferences

There are patterns of morphology common to the general habitat types described here. Those moa species that preferred the more open habitats, shrubland, or forest margins tended to be the stouter and heavier taxa, e.g., *Euryapteryx* and *Pachyornis*. Their relatives that inhabited dense forest, e.g., *Anomalopteryx didiformis* and *Dinornis novaezealandiae* were much more slender and lightly built. This trend therefore parallels that suggested by Haast (1872) and Duff (1952).

Of all moa species only *Megalapteryx didinus* is known to have had feathered tarsi. A majority of birds including many that live in snow regions do not have feathered tarsi but, apart from eagles, those that do have feathered tarsi, e.g., Ptarmigan (*Tetraonidae*) and Darwin's rhea (*Pterocnemia pennata*), inhabit areas periodically subject to snow cover. The Common rhea, (*Rhea americana*) and all other ratites, rarely spend much time in snow and do not have feathered tarsi. That *M. didinus* does is additional support for a montane-subalpine habitat. Its light build and extra long toes (see Worthy 1988b) may either facilitate its ability to walk on soft substrates, be it snow or moss (the latter commonly forms a thick ground cover in wet montane forests), or increase its ability to move over rough surfaces often encountered in upland-subalpine areas.

Compared to other moa species, the species of *Euryapteryx* and *Emeus crassus* exhibit relative shortening of the toes and reduction in the number of phalanges in digit 4, and the ventral surface of the terminal phalanx is flat. This trend is common to birds adapted to a cursorial life and is most advanced in ostriches (*Struthio* spp.) which have only two short toes. The forest dwelling cassowaries (*Casuarius* spp.) have longer toes than the savannah inhabiting emus (*Dromaius novaehollandiae*). Thus, toe morphology of the moa species is consistent with the ecological preferences here described, as the *Euryapteryx* species and *E. crassus* are here inferred to prefer relatively open habitats such as shrublands and grasslands.

Conclusion

The distribution and relative abundance data reveal patterns among moa species which, when correlated with general climatological and past vegetation patterns, enable broad ecological preferences for different moa species to be described. Although "forest" describes the probable preferred habitat of most moa species there is a marked distinction between the fauna of the wet dense, as opposed to the dry, open forest type. Some species preferred forest margins or low shrubland and these species probably proliferated during the Otira Glaciation when such habitats were more widespread. This group of species could undoubtedly utilise grasslands. It is thus no longer tenable to describe the moa as a forest or a grassland bird; each of the eleven species was adapted to a particular niche. Of the 11 species I accept, 7 occurred in the North Island and 9 in the South Island and, as I have demonstrated, some species preferred dense forests and others more open habitats. This synopsis conforms remarkably well with the suggestions of Flux (1989). Using biogeographic theory he suggested that there should have been 8 to 12 moa species that were evenly distributed between forest and open country. Thus, the radiation of moas is not much more spectacular than that of the acanthisittids, or New Zealand wrens, where there were five North Island and six South Island species.

When humans settled New Zealand, at least half the species had restricted distributions so it is not surprising they were quickly extirpated. The little bush moa (*Anomalopteryx didiformis*) and the large bush moa (*Dinornis novaezealandiae*), the two species that ranged over the greatest area at the time of man's arrival, were probably the last species to be driven to extinction. However, the upland moa, (*Megalapteryx didinus*), because it ranged into the inhospitable subalpine zone, may have also persisted after other species were gone.

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Appendix 1 Moa taxa, minimum number of individuals (MNI), and relative proportion (%) from various swamps in Canterbury region.

Taxa	Glenmark Haast 1869 A MNI	%	Motunau McKay 1882 B %	Albury Park Scarlett 1969 MNI	%	Pyramid Valley Anderson 1989 MNI	%	Broken River NMNZ Colln C MNI	%	Molesworth Anderson 1989 MNI	North Dean Burrows et al. 1984 MNI
Anomalopteryx didiformis	–	–	–	–	–	–	–	2	6.2	1	–
Megalapteryx didinus	–	–	–	–	–	–	–	–	–	–	–
Pachyornis elephantopus	22	15.3	90	22	36.2	17	10.4	8	25.0	1	3
Emeus crassus	82	57.0	*	34	55.7	60	36.6	11	34.4	–	3
Euryapteryx geranoides	17	11.8	*	–	–	20	12.2	–	–	3	5
Dinornis struthoides	12	8.3	–	2	3.3	4	2.4	6	18.8	7	–
Dinornis novaezealandiae	3	2.1	*	–	–	8	4.9	4	12.5	2	1
Dinornis giganteus	8	5.5	–	3	4.9	55	33.5	1	3.1	–	1
Total	144			61		164		32		13	14

A. I have here interpreted Haast's identifications, in light of subsequent taxonomic changes, to provide the modern equivalent as follows: *D. casuarinus* and *D. didiformis* equals *Emeus crassus*; *D. elephantopus* equals *P. elephantopus*; *D. crassus* equals *E. geranoides*; *D. struthoides* and *D. gracilis* equal *D. struthoides*; *Palapteryx ingens* and *D. robustus* equal *D. novaezealandiae*; *D. giganteus* and *D. maximus* equal *D. giganteus*.
Scarlett (1969) recorded *A. didiformis* and *M. didinus* to be present in Glenmark, although rare. It is probable that Haast's subsequent excavations revealed these species. Since skeletons from Glenmark were traded world-wide by Haast the remaining collections in New Zealand probably do not represent the excavated relative frequency of species that this first listing by Haast does.
B. McKay alludes to the presence of two species but only lists one. I have indicated (*) the modern equivalents of additional taxa listed by Hutton (1892:150).
C. Identifications are mine.

Appendix 2 overleaf ⇒

Appendix 3 Moa taxa, minimum number of individuals (MNI), and relative abundance (%) from selected North Island swamp sites.

Taxa	Poukawa (A) MNI	%	Te Aute NMNZ (B) MNI	%	Te Aute CM (C) MNI	Te Aute Park 1988 Drain Site	(D) Bed of Lake	Makirikiri Worthy 1989d MNI	%	Clevedon Millener 1981 MNI	%
Anomalopterxy didiformis	14	17.3	1	2.5	1	?	?	181	64.0	20	60.6
Pachyornis mappini	52	64.2	6	15.0	2	?	?	24	8.5	2	6.1
Euryapteryx geranoides	–	–	–	–	5	?	?	?1	–	–	–
Euryapteryx curtus	3	3.7	18	45.0	7	many	none	?1	–	10	30.3
Dinornis struthoides	6	7.4	6	15.0	7	9	12	20	7.1	1	3.0
Dinornis novaezealandiae	3	3.7	3	7.5	4	53	15	47	16.6	–	–
Dinornis giganteus	3	3.7	6	15.0	4	22	1	11	3.9	–	–
Total	81		40		30			283		33	

A. I have checked the identity of bones registered in the NMNZ collections between the numbers S 2696 and S 22453 and calculated the MNI shown here for all bones from this large site. The age range is from about 8000 years BP to the present.
B. The MNI represented by Te Aute bones present in NMNZ was calculated after reidentification of the following specimens: NMNZ S (labelled DM) 99–101, 103–105, 107–113, 115–117, 121, 153–155, 158, 24385–61, 24461.
C. MNI from bones in the CM reported by Millener (1981). Those bones he listed as *E. geranoides* are *P. mappini* (Worthy 1987).
D. James Park listed measurements of bones he collected from Te Aute (Drain and lake bed) in a report to Hamilton dated August 15 1888 (preserved in Hamilton files, NMNZ). Using his measurements and identifications I have determined the total number of femora, tibiotarsi, and tarsometatarsi present for each of the currently accepted *Dinornis* species. Because of overlapping size ranges no attempt has been made to determine numbers of other bones measured by Park for each of the presently accepted emeid species.

Appendix 2 Moa taxa, number of tarsometatarsi (TMT) or minimum number of individual (MNI), and relative proportions (%) from Otago and Southland swamps.

	Hamiltons Hutton 1875				Enfield Hutton 1896a		Kapua Hutton 1896b		Herbert NMNZ Colln		Hamilton's Swamp Winton		Scaifes Lagoon Wanaka Trotter 1970		Remarkables Hamel 1977	Owaka Hamel 1977	Clinton Hamel 1977	Paerau Otago Museum	
	A		C		B		B		C		C							C	
Taxa	TMT	%	MNI	%	TMT	%	TMT	%	MNI	%	MNI	%	MNI	%	MNI	MNI	MNI	MNI	%
Anomalopteryx didiformis	–	–	–	–	–		4	0.5	–		3	7.5	–	–	1	–	–	–	–
Megalapteryx didinus	–	–	–	–	–		3	0.5	–		1	2.5	–	–	1	–	–	–	–
Pachyornis elephantopus	52	31.1	14	22.6	47	12.8	63	8.4	3	11.1	–	–	–	–	1	5	–	103	51.7
Pachyornis australis	–	–	–	–	–	–	–	–	–	–	1	2.5	–	–	–	–	–	–	–
Emeus crassus	32	19.2	21	33.9	193	52.4	399	53.3	8	29.7	6	15.0	–	–	1	1	6	10	5.0
Euryapteryx geranoides	57	34.1	22	35.4	94	25.5	156	20.8	11	40.7	5	12.5	5	41.7	2	1	2	29	14.6
Dinornis struthoides	18	10.8	4	6.4	19	5.2	55	7.3	2	7.4	5	12.5	5	41.7	2	–	–	3	1.5
Dinornis novaezealandiae	8	4.8	1	1.7	4	1.1	39	5.2	3	11.1	6	15.0	1	8.3	1	–	–	1	0.5
Dinornis giganteus	–	–	–	–	11	3.0	30	4.0	–	–	2	5.0	1	8.3	–	–	–	–	–
EMEIDAE sp. indet.	–	–	–	–	–		–		–	–	7	17.5	–	–	–	–	–	53	26.7
Dinornis sp. indet.	–	–	–	–	–		–		–	4	10.0	–	–	–	–	–	–	–	–
Total	167		62		368		749		27		40		12		9	7	8	199	–

A. Here bones identified as *D. robustus* and *D. ingens* are called *D. novaezealandiae; D. rheides, D. didiformis*, and *D. casuarinus* together equal *Emeus crassus; D. crassus, D. crassus* var. *major*, and *D. gravis* equal *Euryapteryx geranoides; D. elephantopus* and *D. elephantopus* var. *major* equals *Pachyornis elephantopus*.

This interpretation is veritifed by Hutton (1986: 628) who repeats his previous list using the then current taxonomy.

Only numbers of tarsometatarsi are listed here to illustrate relative abundance.

B. *Meionornis casuarinus* and *M. didinus* are here listed as *Emeus crassus; D. maximus* as *D. giganteus; D. robustus* as *D. novaezealandiae; D. torosus* as *D. struthoides; Eurapteryx crassa, E. ponderosa*, and *E. gravis* as *E. geranoides; Pachyornis immanis, P. elephantopus*, and *P. habilus* as *P. elephantopus*.

C. Species determination by myself. Many bones from Hamiltons (Hutton 1875) are no longer present in the Otago Museum, or are not identifiable as derived from Hamiltons. I identified 189 bones. The largest bones of *Euryaptheryx* had been identified as *Pachyornis* but otherwise the treatment (A above) appears to be justified. Hamilton's Swamp at Winton is a separate site to that at Hamiltons on the Manioto Plain. Material from the Winton site is preserved in the Southland Museum. The Paerau site is O'Malley's Swamp and is close to Hamiltons on the Manioto Plain. The MNI listed here are obtained from identificationsn of 846 femora, tibiotarsi and tarsometatarsi from this ste in the Otago Museum.

Appendix 4 Minimum numbers of individuals (MNI) of moas represented in selected North Island archaeological collections for which the author has examined and identified material.

	Paremata MNI	Makara MNI	Foxton MNI	Kaupo-konui MNI	Ohawe MNI	Opua MNI
Anomalopteryx didiformis	18	2	10	11	–	2
Pachyornis mappini	2	2	8	10	1	3
Euryapteryx geranoides	1	–	1	5	–	1
Euryapteryx curtus	–	3	11	31	4	5
Dinornis struthoides	2	–	–	–	–	–
D. novaezealandiae	2	1	2	–	–	–
D. giganteus	1	–	1	2	1	–
Total	26	8	33	59	6	11

Paremata—combined Sinclair and Davidson collections (NMNZ). Makara—material reported on by Yaldwyn (1959.

Foxton (148/1)—Bruce McFadgen's collection (NMNZ) determined after analysis of all moa bones irrespective of layer and is inclusive of Lindsey and O'Leary's initial collection and that of T. Barrow. Among bones of the three most common species at Foxton there were markedly fewer tarsometatarsi than tibiotarsi or femora of *A. didiformis* and *P. mappini* in contrast to bones of *E. curtus* where all elements were roughly equally represented. This suggests *E. curtus* was killed close to the site and the other species some distance away.

Kaupokonui—Taranaki Museum collection derived from R. Cassels 1974 excavation, D. Foley 1979 collection and surface collections of May 1976, 5 June 1980, and June 1981. It excludes material from Buist and Scarlett's 1963/67 excavation which could not be located.

Ohawe (=Waingongoro)—Taranaki Museum collection from the excavations of Mrs T. Canavan in 1972.

Opua—Taranaki Museum collection collected by M. G. Maxwell in 1907 (Fyfe 1988).

Appendix 5 Determination of the moa species present and their frequency in the collection made by Walter Mantell in 1843 at Waingongoro, South Taranaki.

Richard Owen received this collection and in 1848 reported on them in the Transactions of the Zoological Society London, Volume 3, page 346. He tabulated the bones from Waingongoro (=Ohawe) into the following species: *Dinornis casuarinus*, *D. didiformis*, *D. curtus*, *D. dromioides*, *D. geranoides*, *D. ingens*, *D. giganteus*. At this time Owen had incorrectly associated femora of *E. curtus* with *A. didiformis* and femora of *A. didiformis* as *D. dromioides*. Later figures of femora (Plate 65, figures 5 and 6—Transactions Zoological Society of London Volume 5 (1866) and tarsometatarsi (Plate 67, figures 5 and 6 (captioned as *D. geranoides* are in fact *P. mappini*. So it appears that Owen incorrectly associated leg bones of P. mappini with the type skull of *D. geranoides*. *D. casuarinus* (= *Emeus crassus*) does not occur in the North island and it is probable that bones listed for this species had the size and stoutness of *crassus* so probably were *D. geranoides*.

Based on the above facts and assumptions I have derived the following MNI for the moa species as now recognised: *A. didiformis*—7; *E. curtus*—9; *E. geranoides*—1, *P. mappini*—10; *D. novaezealandiae*—2; *D. giganteus*—1. The species apparently present and their frequency is very similar to that which I subsequently determined for other south Taranaki sites (Appendix 4), thus despite the pitfalls of this analysis I believe it probably approaches reality.

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The diet of feral cats (*Felis catus* L.) on Hawke's Bay farmland, New Zealand

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Abstract Food remains were analysed in 361 cat faeces (scats) collected from September 1983 to May 1987 on farmland in southern Hawke's Bay. Mammals were the most important food items in scats, both by occurrence (76%) and by weight (74%). House mice were the most frequently (50%) encountered remains, and comprised only 12% of the total prey identified by weight; rats were less frequently found (20%) but the most important item by weight (39%). Other mammals found were scavenged possums (13% by weight), sheep (7%), and lagomorphs (3%). Birds, consisting mainly of introduced species, including turkeys, were both frequent (24%) and important by weight (24%). Invertebrate remains consisted mainly of cicada nymphs (Homoptera) (10% by frequency), grass grubs (Coleoptera) (8%), and black field crickets (Orthoptera) (7%) contributed less than 2% by weight. Cicada nymphs were recorded only in willow/swamp habitat. No significant differences were found between vertebrate prey recorded in scats from willows and swamps and vertebrate prey from barns and pasture. There were no consistent local or seasonal changes in frequency of occurrence of rats, but mice were found more frequently in scats collected in winter. Possum remains were found mainly in winter. Birds were the main items in scats collected in the spring and summer months. Eggs of *Toxocari cati* (64%) were the only identifiable internal parasite frequently found in the scats.

Keywords feral cat; *Felis catus*; farmland; diet; scats; mammals; birds; invertebrates; parasites

INTRODUCTION

This paper describes the diet of about 15–20 resident feral cats (*Felis catus*), observed from September 1983 to May 1987 on Hawke's Bay farmland, New Zealand. The cat arrived in New Zealand with European explorers, sealers, and whalers in the latter part of the 18th century (Thomson 1922; Druett 1983; King 1984; Lever 1985). At first, they stayed close to towns, but native birds provided an easy source of food. With the increase of introduced rodents and rabbits, *Oryctolagus cuniculus*, and the deliberate transportation and release of cats into the countryside after the 1870's (Druett 1983), cats became widespread throughout New Zealand and its offshore islands (Wodzicki 1950; Collins & Charleston 1979). The impact of the feral cat on rabbit populations in New Zealand has been described briefly by Gibb et al. (1969, 1978), but the most extensive information on their diet available at present is given by Fitzgerald & Karl (1979) from a forested area 18 km east of Wellington. There are a number of other studies of cat diets from New Zealand offshore islands: Little Barrier (Marshall 1961); Campbell (Dilks 1979); Stewart (Karl & Best 1982); and Herekopare (Fitzgerald & Veitch 1985).

The feral cat is the primary host of several protozoans, especially *Sarcocystis* spp., which use several species of herbivorous mammals as intermediate hosts. The species found in sheep (*S. gigantea* and *S. medusiformis*) (Collins et al. 1979) are spread by cats feeding from dead sheep or lambs (Collins & Charleston 1979). The details of the protozoan parasites of cats will be the subject of another paper (Langham & Charleston, unpubl. data).

The information on cat diet presented in this paper was collected during a study of the movements of feral cats and their role in the spread of *Sarcocystis*. The opportunity was taken to identify and quantify prey remains in the scats collected for detection of sporocysts of *Sarcocystis*, and to document seasonal and annual changes in cat diet.

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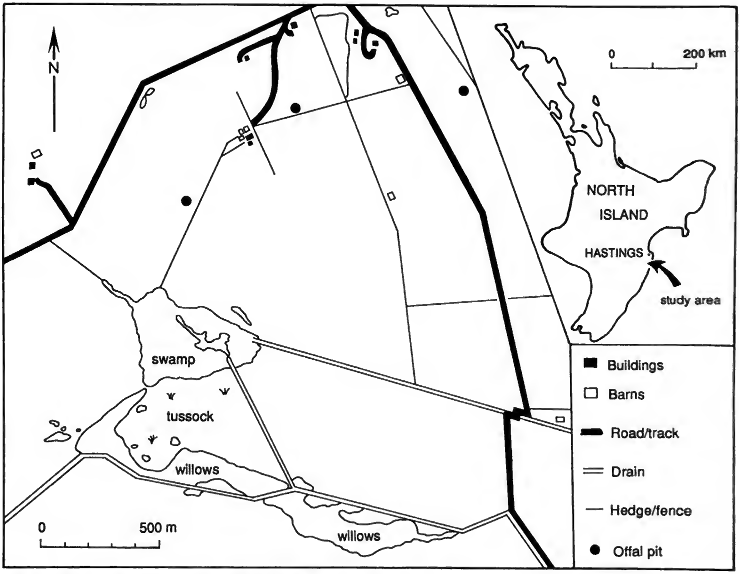


Fig. 1 Study area showing main drains, roads and farm buildings.

STUDY AREA

The feral cats were studied on 5 km^2 of farmland about 12 km south-west of Hastings, Hawke's Bay, on the east coast of the North Island of New Zealand (Fig. 1). This part of the Heretaunga Plains is mainly devoted to grazing of sheep and beef cattle, although a few fields each year are planted for crops of legumes, cereals, brassicas, and carrots. The farmland is dissected by ditches draining a swamp and stream. The swamp contains a small lake surrounded by dense vegetation, mainly of cabbage trees *Cordyline australis*, blackberry *Rubus fruticosus*, willow *Salix* spp., poplars *Populus* spp., flax *Phorium tenax*, and grasses and sedges. Between the swamp and the main drain is a paddock that is frequently waterlogged. Along both sides of the drain and connecting the swamps are groups of willows (Fig. 1). The rest of the area consists of grassed paddocks, many with windbreaks of poplars and cypresses *Cupressus macrocarpa*, and a few with hedges of boxthorn *Lycium ferocissimum*. North of the swamp there are several offal pits for the disposal of unwanted carcasses which are often left uncovered until they are burnt. Barns and various farm buildings, including homesteads, are found on the drier section to the northwest.

The study area is surrounded by low hills to the south and northwest. It experienced strong west-to-northwest foehn winds with clear skies, giving warm sunny days but cool nights. Meteorological observations in the study area for the years 1983–1987 show that extremes of temperature ranged from 30°C during the day to 7°C at night in summer (November–February), with a mean minimum grass temperature of about 5°C. In winter (May–August), the temperature ranged from about 16°C during the day to −2.5°C at night and a grass minimum of −4.0°C. In July, ground frosts occurred on average about 15 days. The extremes of temperature in winter often lead to fogs in the low-lying areas at night and in the early morning. Humidity ranged from about 40% during the day to up to 100% at night in winter, and from 30% to 95% in summer. The annual rainfall recorded at Havelock North, 15 km northeast, was on average about 660 mm from 1983 to 1987 (J.P.C. Watt, pers. comm.). In 1985, the annual rainfall was 890 mm, with 240 mm in July. On 25–26 July, 151 mm of rain fell in 48 h. This caused extensive flooding, which resulted in the death of about 400 lambs and the disappearance of about 100 marked possums *Trichosurus vulpecula* (G.D. Ward, pers. comm.). No cats disappeared or died during this period. The summers were dry, with an average of 42 mm of rainfall/month from 1983 to 1986. During the other seasons of the year, for the same period (excluding 1985), the average rainfall was 67 mm/month.

Prey abundance

Rabbits and hares *Lepus europaeus* were uncommon in the study area (0.05/ha), with only a few being recorded, usually near cover. Rodents included ship rats *Rattus rattus*, Norway rats *R. norvegicus*, and house mice *Mus musculus*. Ship rats were the most abundant of the three, especially in the willows and undergrowth; Norway rats mainly frequented offal pits, buildings, and the wetter areas, mice appeared to be widespread. No estimate was made of the numbers or density of rodents.

Seed-eating passerines, such as the house sparrow *Passer domesticus*, goldfinch *Carduelis carduelis*, and yellowhammer *Emberiza citrinella*, were abundant, feeding in the open fields and nesting in windbreaks. The skylark *Alauda arvensis* was common on the surrounding hills. In the more vegetated areas such as the willows, blackbirds *Turdus merula*, song thrushes *T. philomelos*, fantails *Rhipidura fuliginosa*, grey warblers *Gerygone igata*, and silvereyes *Zosterops lateralis* were found. Also on the farmland, there was a population of about 100–150 adult free-range turkeys *Meleagris gallopavo*, which nested either in barns or in long grass at the edges of paddocks and roosted in trees or on farm gates at night.

Possums were common in the study area, denning in the swamp, willows, and barns. Densities recorded in open farmland were 0.07/ha, in the swamp 14/ha, and in the willows about 5–8/ha (G.D. Ward, pers. comm.). The remains of possums found in cat scats appeared to be adults judging from their claws and teeth. The aggressiveness, size of independent possums (1.0–3.5 kg), and their tree-climbing ability would make them a difficult prey for cats. As the main mortality of possums occurs in the autumn and winter when they are most frequent in cat scats, it is most likely that the cats either scavenged on dead possums, or killed those in very poor condition.

No survey was made of insects, but evidence from scats suggests that the most common species—cicadas, grass grubs *Costelytra zealandica*, and black field cricket *Teleogryllus commodius*—are seasonally abundant.

METHODS

The numbers and movements of cats were recorded by trapping and radio telemetry. Sightings were rare, especially in the wooded and long-grass habitats, and could only be used to supplement other methods. Cats were categorised either as transients (trapped only once) or residents (trapped regularly over several months or radio tracked for at least 3 months in the study area). Radio tracking involved both daily fixes, usually when cats were resting in dens, and night tracking using a triangulation method from two tracking stations. Over 24 h periods, home ranges averaged about 100 ha for those females in the swamp and willows, but about 240 ha for those females denning in barns, who had to move much further to suitable hunting areas such as long vegetation or offal pits. Males had home ranges of about 250 ha. Further details of home ranges are included in a separate paper (Langham & Porter, unpubl. data).

There have been many studies on the diet of cats using a variety of methods (see Fitzgerald & Karl 1979; Fitzgerald 1988). The present work is part of a wider ecological study which relied on observations of living animals, so it was not possible to analyse stomach contents. The studies of Nilsson (1940), Hubbs (1951), Goldschmidt-Rothschild & Lups (1976), Borkenhagen (1978), Jones & Coman (1981), and Niewold (1986) all used stomach contents to study the diet of cats, so their results are not directly comparable to mine. The secretiveness of cats in this area made it impossible to retrieve or observe the prey items brought in, a method used with rural domestic cats by Borkenhagen (1978) and Churcher & Lawton (1987). The examination of scats is a well-tried method, used in North America (Jackson 1951), Europe (Liberg 1984), Australia (Triggs et al. 1984), New Zealand (Gibb et al. 1969, 1978; Fitzgerald & Karl 1979), and various islands around

Table 1 Mean weights of food items used in calculating contribution by weight in cats scats, based on Fitzgerald & Karl (1979).

Prey items	Weight (g)
Mammals	
Ship rat *Rattus rattus*	125
Norway rat (young) *Rattus norvegicus*	125
House mouse *Mus musculus*	15.5
Rabbit *Oryctolagus cuniculus*	170*
Hare *Lepus europaeus*	170*
Hedgehog (young) *Erinaceus europaeus*	50
Sheep (scavenged) *Ovis aries*	170*
Birds	
Song thrush *Turdus hilomelos*	70
Blackbird *Turdus merula*	90
Skylark *Alauda arvenis*	30
House sparrow *Passer domesticus*	25
Yellowhammer *Emberiza citrinella*	25
Goldfinch *Carduelis carduelis*	20
Chaffinch *Fringilla coelebs*	20
Hedge sparrow *Prunella modularis*	20
Grey warbler (N) *Gerygone igata*	6.5
Fantail (N) *Rhipidura fuliginos*	8
Sivereye (N) *Zosterops lateralis*	11.5
Unidentified large passerine	90
Unidentified medium passerine	20
Unidentified small passerine	10
Paradise ducklings (N) *Tadorna variegata*	100
Mallard *Anas platyrhynchos*	170*
Pheasant *Phasianus colchicus*	170*
Turkey *Meleagris gallopavo*	170*
Turkey *Meleagris gallopavo*	170*
Feral pigeon *Columba livia*	170*
Black swan *Cygnus atratus*	170*
Fish	
Small unidentified	10
Invertegrates	
Cicada (nymph)	0.7
Cockroach *Periplaneta australasiae*	0.8
Black field cricket *Telegryllus commodus*	0.6
Grass grub beetle *Costelytra zealandia*	0.5
Porina moth larvae *Wiseana cervinata*	0.1
Gum emperor moth larvae *Antheraea eucalypti*	0.3
Centipede	1.0
Spider	0.2
Collembola	0.1
Small snail	0.3

*represents approximate daily intake by a cat
N = native species

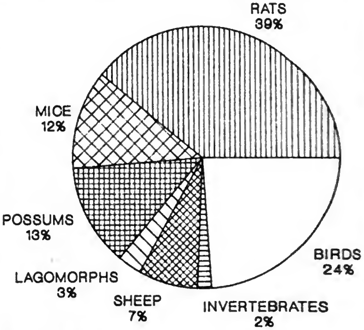


Fig. 2 Percentage frequency of occurrence of main food items in cat scats.

the world (Marshall 1961; Jones 1977; Karl & Best 1982; Apps 1983; Konecny 1987).

Initially, scats were collected around the swamp and in and around barns, including some on straw or in sand-filled trays provided. More scats were collected along the drain between the willows in 1986, after radio tracking showed that this was one of the main regions frequented by cats. The cats favoured certain areas and these we visited several times a week. Most scats found on the farmland were on bare earth; in contrast, scats in the Orongorongo Valley are often found on tufts of grass (B.M. Fitzgerald, pers. comm.). Almost all scats collected were uncovered, probably placed deliberately as markers to other cats (see MacDonald 1985). Some covered scats may have gone undetected, but there was no sign of scratch marks in the areas visited.

On collection, scats were sealed in labelled plastic bags and frozen. For analysis, scats were thawed, soaked overnight in weak NaOH (2% solution), and washed in a fine sieve (<0.5 mm mesh). The contents were placed in alcohol, then examined and sorted by eye and binocular microscope. Mammals were identified from bones (especially jawbones), teeth and claws, and by microscopic characteristics of the hair or fur (Day 1966; Brunner & Coman 1974). An impression of the scale pattern was obtained when the hair was placed on a film of gelatin on a microscope slide. This scale pattern was sufficient to recognise the species of mammal when used together with length, waviness, and colour pattern. If a scat contained only hair of one mammal species this was assumed to represent one individual. As skeletal remains were insufficient to distinguish between the rat species, fur often made identification possible. The wear of teeth of Norway rats in the scats indicated they were mostly from young individuals, and they have been grouped with ship rats in this account. Birds could sometimes be identified from bones and size, colour, and form of feathers, although feet and claws were the most frequent parts represented. When their identity was doubtful, birds were classified into large (Galliformes, Anatidae), medium (Turdidae), and small (Alaudidae, Ploceidae, Fringillidae, Sylvidae, Muscicapidae). There may have been some Starlings *Sturnus vulgaris* among the medium-sized birds, although domestic cats observed by the author seem to find the flesh unpalatable. Invertebrates were mostly insects, identified from their chitinous remains, and the remainder were grouped together as "other invertebrates".

The results of scat examinations were analysed using two methods: (1) frequency of occurrence, i.e., the percentage of scats in a sample containing a particular prey item or group; and (2) frequency by weight, i.e., the percentage of the total weight of each of prey item contained in a group of scats. To load the frequencies according to the number of prey, each item was multiplied by the mean weight given by Fitzgerald & Karl (1979) (Table 1). It was assumed that large prey items contributed only 170 g each to the daily food intake, and that the cats defaecated once a day (Howard 1957; Scott 1965; Fitzgerald & Karl 1979).

The study area could be divided into two habitat types: (1) barn/pasture where cats used barns as den sites and hunted across pasture, offal pits, fence lines, and windbreaks; and (2) willow/swamp where cats used hollow or fallen trees and dense vegetation as den sites, and hunted in tall vegetation and beside drains and the swamp. Radio fixes indicated that of the 12 females radio collared, 6 spent most time in the willow/swamp habitat and rarely moved to the barn/pasture habitat occupied by the other 6 females. Although 12 males were less restricted in movement, 4 were only recorded in the willow/swamp habitat and 6 were only recorded in the barn/pasture habitat. Therefore, the scats found in each habitat were likely to contain remains of organisms caught within that habitat.

RESULTS

From September 1983 to May 1987, 361 scats were collected (Table 2). Allowing for monthly variations, the samples in 1984, 1985, and 1986 were sufficient to allow a comparison of the annual distribution of prey animals (Table 3).

Mammals

Mammals were the most important item both by number and by weight in the diet of feral cats (Table 3, Fig. 2).

Rodents were the most important single group represented, contributing over 50% by weight (Table 4, Fig. 2). Mouse remains were found in scats throughout the sampling period, but were most numerous in autumn and winter (Tables 5, 6; Fig. 3).

Table 2 The number of scats collected by month from 1983 to 1987.

	Month												
Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
1983									4	3	5	3	15
1984	7	2		1	1	11	21	6	10	11	5	1	76
1985		1	2	3	13	11	11	8	6	2	4	1	62
1986	6	33	19	10	7	11	14	36	16	6	9	16	183
1987	2		10	12	1								25
Total	15	36	31	26	22	33	46	50	36	22	23	21	361

Table 3 The percentage frequency of occurrence of prey items in scats for 1984, 1985, and 1986.

		Mammals					Birds			Invertebrates			
Year	No. scats	Rats	Mice	Possums	Lagomorphs	Sheep	Large	Medium	Small	Cicadas	Beetles	Crickets	Other
1984	76	15.8	48.7	1.3	–	1.3	6.6	6.6	19.7	–	13.2	2.6	14.5
1985	62	19.4	64.5	12.9*	3.2	3.2	1.6	1.6	16.1	–	6.5	3.2	8.1
1986	183	19.7	45.4	4.4	1.1	3.8	4.9	6.6	20.8	18.6	7.1	6.6	4.9
Total	321	18.7	49.8	5.3	1.2	3.1	4.7	5.6	19.6	10.6	8.4	5.0	7.8

*Only possums were significantly more frequent in scats in 1985 ($\chi^2 = 9.25$, $P < 0.01$ for 2 d.f.)

Table 4 The percentage frequency of occurrence and the percentage by weight of prey in feral cat scats, all years pooled.

Prey item	Number of scats found	% occurrence*	% by weight
Mammals			
Mice	181	50.1	12.2
Rats	72	19.9	39.1
Possums	17	4.7	12.6
Lagomorphs	4	1.1	3.0
Sheep	10	2.8	7.4
Total			74.3
Birds			
Large	17	4.7	11.3
Medium	19	5.3	7.0
Small	75	20.8	5.6
Total			23.9
Invertebrates			
Cicada	36	10.0	0.9
Coleoptera	30	8.3	0.5
Orthoptera	26	7.2	0.2
Total			1.6
Other items	33	9.1	0.2
Total	361	–	100.0

*Some scats contain more than 1 item from each group.

Mice were found in 25–30% of the scats in spring and summer, but this increased to 60–70% in autumn and winter, giving an overall occurrence of 50% (Table 5). Incisor teeth of rodents were not digested by cats and this allowed the number of animals in a scat to be counted. Most scats with mouse remains contained only one individual (88%, $n = 181$), but 15 scats contained 2 mice and 6 contained the remains of 3. The highest frequency recorded was 1.6 mice per scat in spring 1984. In this sample, 16 scats from farmland contained both rats and mice. A single rat and mouse were found in 11 scats, but the remaining 5 each contained 2 mice and 1 rat. Their teeth indicated that two of these five rats were young ("0"–year class). The number of scats containing mice is significantly higher in autumn and winter compared with spring and summer ($\chi^2 = 27.2$, $P < 0.001$, 1 d.f.) (Table 5). Mice contributed about 17% of the estimated prey in autumn and winter compared with less than 7% in spring and summer (Table 6). Although mice were more abundant, they contributed more biomass to the diet than did rats only in winter 1984 (Fig. 5).

Rats were rarely more numerous than mice (Fig. 3), but usually contributed at least 30% of the biomass in the diet in any one season (Table 6). Apart from the scats containing the remains of rats and mice, a further 53 scats each contained one rat, and one had the remains of two rats. In spring 1984, the biomass

Table 5 The percentage frequency of occurrence of prey items in cat scats by season.

Prey item	Season Spring	Summer	Autumn	Winter	Total	N
Mammals						
Rats	25.9	20.8	20.3	15.5	19.9	72
Mice	29.6	25.0	62.0*	69.8*	50.1	181
Lagomorphs		1.4	2.5	0.8	1.1	4
Possums	3.7	1.3	1.3	9.3**	4.7	17
Sheep	2.5		3.8	3.9	2.8	10
Birds						
Large	6.2	12.5	2.5	0.8	4.7	14
Medium	4.9	11.1	2.5	3.9	5.3	19
Small	28.4	22.2	20.3	15.5	20.8	75
Invertebrates						
Cicadas		40.3	8.9		10.0	36
Coleoptera	14.8	18.1	3.8	1.6	8.3	30
Orthoptera	2.5	2.8	25.3	1.6	7.2	26
Other	11.1	5.6	12.7	7.8	9.1	33
Number of scats	81	72	79	129	**361**	517

N = number of items

*Mice significantly more abundant in autumn and winter ($\chi^2 = 27.2$, $P < 0.001$ for 1 d.f.)

**Possums significantly more abundant in winter ($\chi^2 = 8.90$, $P < 0.01$ for 1 d.f.)

of rats rose to over 55% of the total, and in autumn 1987 it was nearly 80% ($n = 23$) (Fig. 5).

Scats that contained rodents seldom contained other prey as well. In three scats, one rat, one mouse, and remains of a small bird were found. In six scats, remains of one rat were recorded, together with those of a small bird in four, and a blackbird or songthrush in each of the other two. In contrast, there were 19 scats in which mouse remains coincided with those of a bird, 15 of these were with small birds, 3 with blackbirds or songthrushes, and 1 with a turkey. Mouse remains were found in the same scat with rabbits twice, with sheep wool four times, and with possums six times. One exceptional scat included remains of a mouse, a rabbit, a small bird, and sheep's wool. In another scat, a mouse was found with the remains of a small, unidentified fish.

Possums occurred in 4.7% of the scats and contributed 12.6% of the biomass (Table 4). More possums were eaten in 1985 ($\chi^2 = 9.25$, $P < 0.01$, 2 d.f.). The higher incidence of possums occurred in July 1985 which coincided with a cold, wet period (151 mm of rain occurred on 25–26 July), during which about 100 marked possums disappeared. The remains found in cat scats were probably the result of cats scavenging on dead animals. Possums were significant dietary items in cat scats in August 1986 (Fig. 4) which also coincided with a cold, wet period. In 1986, three times as many scats were collected than in 1985, so possums occurred about three times as frequently in 1985 (Table 3). In August 1986, four and a half times as many scats were collected than in August 1985 which accounts for the August 1986 peak in Fig. 4. Possums were significantly more important in winter, occurring in 9.3% of the scats ($\chi^2 = 8.90$, $P < 0.01$, 1 d.f.) (Table 5) and contributing about 26% of the biomass for that season (Table 6).

Fourteen possums (82%, $n = 17$) were recorded in scats from the willow/swamp area where the highest density of possums were recorded, coinciding with the abundance of their den sites.

Lagomorphs were rare on farms and in scats. Only three scats contained remains of rabbits, one those of a hare, representing only 3.0% by weight of the total items consumed (Table 4, Fig. 2). Sheep's wool in the scats indcated that cats scavenged from dead sheep or lambs. In an experiment, sheep and lamb carcasses were placed in areas where cats had been radiotracked. Each carcass was surrounded by soft sand to record the tracks of visiting animals. Although cats did visit most of the carcasses, they scavenged only from those whose flesh was exposed, as in, for example, those discarded after skinning or those that had been plucked and torn open by harriers, *Circus approximans*, or rats. Of 10 scats containing sheep's wool, three were collected in May and June in the willows where a sheep died after being hauled out of a drainage ditch. This carcass bore evidence of scavenging at about the same time as these scats were collected. Sheep were represented in 2.8% of the scats and contributed 7.4% by weight, assuming that each record of this item represented 170 g of meat, the total daily consumption (see Methods).

Table 6 The estimated percentage frequency by weight of prey items in cat scats by season.

Prey item	Spring	Summer	Autumn	Winter	Total
Mammals					
Rats	48.8	36.0	43.5	32.0	39.1
Mice	6.9	5.4	16.5*	17.8*	12.2
Lagomorphs		3.3	7.4	2.2	3.0
Possums	9.5	3.3	3.7	26.1**	12.6
Sheep	6.3		11.1	10.9	7.4
Birds					
Large	12.6	27.3	7.4	2.2	11.3
Medium	5.8	14.2	3.9	5.0	7.0
Small	8.1	6.1	4.9	3.8	5.6
Invertebrates					
Cicadas		3.8	0.2		0.9
Coleoptera	1.2	0.7	0.1	<0.1	0.5
Orthoptera	0.2	<0.1	0.8	<0.1	0.2
Other	0.5	<0.1	0.3	0.1	0.2
No. of scats	81	72	79	129	361

*and ** significance as in Table 5.

Birds

Few of the fluctuations in frequency of occurrence of birds in cat scats could be distinguished from random variation in the incidence of small passerines (skylarks, sparrows, finches, and warblers). The only exceptions were (a) in the summer and autumn of 1983/84, when four turkeys were eaten, and (b) in the summer of 1986/87 when six blackbirds or song thrushes were taken at the same time as four paradise ducklings from a small pond in the willows area (Fig. 5).

Birds are significantly more common in cat scats in spring and summer than in autumn and winter ($\chi^2 = 11.19$, $P < 0.01$, 1 d.f.). This difference is mainly because of the influence of large-bird remains in the cat scats such as turkeys from the pasture habitat and ducks from the pond in the willows ($\chi^2 = 11.95$, $P < 0.001$ for 1 d.f.) (Table 7). Usually, it was not possible to determine the ages of birds from their remains, but there was an influx of fledglings in

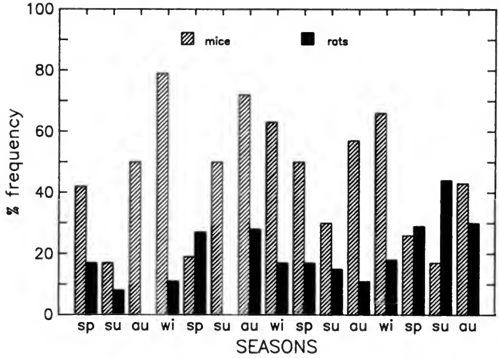


Fig. 3 Percentage frequency by weight of main food items in cat scats.

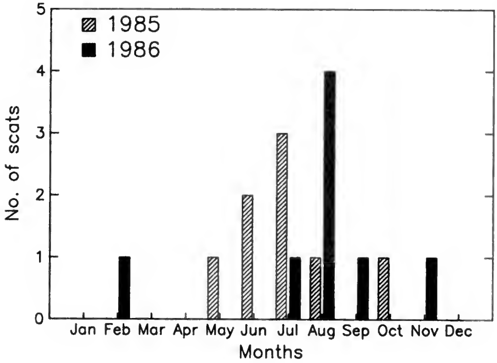


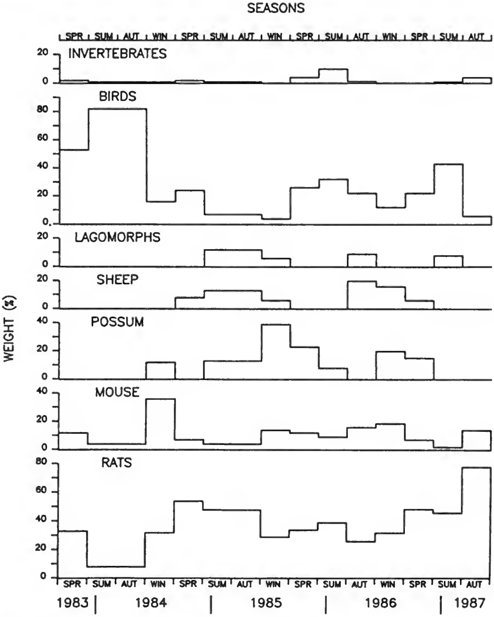
Fig. 4 Number of scats containing possum remains in 1985 and 1986.

spring and summer which are presumably more prone to predation.

There was no difference in the number of large, medium, or small birds found in the scats from the swamp/willows and the pasture habitat, but overall there were more bird remains in the scats from pasture (38.4%, n = 138) than from the swamp/willows (26.0%, n = 223) (χ^2= 4.29, P <0.05 for 1 d.f.). Although there were less bird remains in scats collected in 1985, the difference was not significant (Table 3).

Birds contributed about 24% by biomass to the diet of feral cats, judging from the remains identified in the total scats collected (Table 4, Fig. 2). In 1984 and 1986, the biomass from birds totalled 33.0% (n = 78) and 24.3% (n = 183), respectively, but in 1985

Fig. 5 Seasonal percentage by weight of main food items in cat scats.



only 8.4% ($n = 62$). In 1984, the difference was caused by predation on turkeys and a pheasant which lived on open pasture or stubble, nested in barns, and roosted on gates and low branches of pine trees. These birds contributed 18.1% of the biomass in 1984. It is not known if the adult turkeys were killed or merely scavenged, but cats almost certainly take young hatchlings; few (<5%) survive to fledging. Besides a turkey and a pheasant, mallard ducks and paradise ducklings figured in the cats' diet in 1986 and formed 10.4% of the biomass. The increase in the number of scats collected in the willows close to the main drain led to the bias of remains of aquatic birds in the scats in 1986.

Medium-sized birds identified were either blackbirds or songthrushes, and these represented about 18% by occurrence and 31% by weight of all bird prey. They formed 7% of the biomass of all prey (Table 4). Small birds contributed only 21.7% of the total weight of birds and less than 6% of the total biomass of all prey. The smallest (6–12 g) were native species—fantails, grey warblers, and silvereyes—representing 20 individuals (18%) and about 4% of the biomass of birds. Introduced species—sparrows (Ploceidae), and finches and buntings (Fringillidae), comprised 35 individuals (32%) and 17% of the total biomass of birds. The remaining birds were unidentified nestlings of small birds (13%), and contributed <3% by weight (Table 4). Also, there were two individuals with long hind claws, probably the introduced skylark rather than the less abundant native New Zealand pipit *Anthus novaeseelandiae*.

Invertebrates

Most invertebrates identified in the scats were insects, although there were spiders and small snails in a few samples. Most of the insects identified were from the

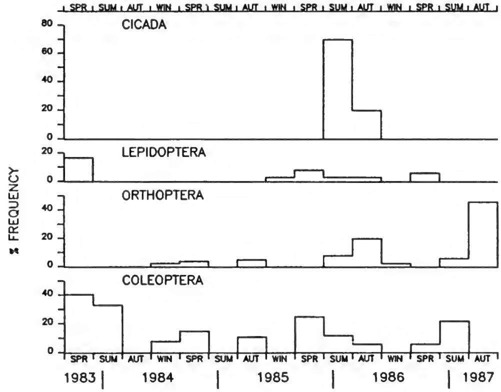


Fig. 6 Seasonal percentage frequency of main insects found in cat scats.

orders Coleoptera, Orthoptera, Lepidoptera, and Homoptera. The only other insects, recorded rarely, were Hymenoptera, Collembola, and Dictyoptera (cockroaches). All the Coleoptera were members of one species, the adult grass grub beetle, which was found mainly in scats collected in the spring and summer months (Fig. 6). Most of the Homoptera belonged to one species of cicada *Amphipsalta zelandica*, which was abundant only in February and March 1986, when cats fed on nymphs emerging from the soil to metamorphose into adults. Of the 33 scats collected in February, 28 contained cicada nymphs (usually identified by their large chitinous front digging claws) (Fig. 6). Eleven scats contained only cicada nymphs, seven had nymphs and a mouse, two had nymphs and a rat, and a further six had nymphs and a small bird. In the remaining two, cicadas were insignificant. By March, cicada nymphs were found in only 7 scats out of 19. Cicadas were therefore important for about a month, and were taken by more than one individual cat, judging by the frequency of scats (12 over one 24 h period). Radio-tracking indicated that at least six different cats were in the area in which these scats were found. Insect abundance was influenced significantly by cicadas, which in February 1986 contributed about 10% of the biomass. Most of the orthopterans belonged on one species, the black field cricket, which was recorded in the scats collected in spring and summer (Fig. 6). Lepidoptera were eaten as larvae and included several species: porina moth *Wiseana cervinata*, common grass moth *Orocrambus flexuosellus*, and occasionally the large larva of the gum emperor moth *Antheraea eucalypti*. Lepidoptera larvae were recorded only in spring and summer. In terms of weight, invertebrates contributed less than 2% of total prey, except when cicada nymphs were taken in February 1986.

Table 7 Number of birds found in cat scats according to season.

	Season				
Size	Spring	Summer	Autumn	Winter	Total
Large birds (170 g+)	5	9***	1	1	17
Medium birds (70–90 g)	4	8	2	5	19
Small birds (10–30 g)	23	16	16	20	75
Total	32	33**	20	26	111
No. of scats	81	72	79	129	361

***$\chi^2 = 11.19$, $P < 0.001$ for 1 d.f. significantly more large birds in spring and summer.

**$\chi^2 = 11.95$, $P < 0.001$ for 1 d.f. signicantly more birds in spring and summer.

Parasites

In the course of scat collection, 65 samples were analysed for parasites. One of the main objectives of lecting scats was to search for sporocysts of *cocystis* spp. for which the cat is the primary st. Most parasites in the scats were probably ived from other prey species such as rodents. In ticular, the eggs of the nematode *Toxocara cati* re found in 64% of the scats. *Sarcocystis* spp. rocysts were found in only 3 (4.6%) of the nples. The details of the parasites in cat scats will reported elsewhere (Langham & Charleston, ubl. data).

SCUSSION

Hawke's Bay farmland between 1983 and 1987, mmals and birds were the main prey items of the al cat, both by frequency of occurrence and by ight. The diet of the cats in this farmland habitat fered markedly from that of cats studied elsewhere New Zealand in that very few lagomorphs but ny rodents were taken as prey. Also, birds, particuly the more common introduced European species, tured much more in the diets of these farmland ts (24% by weight) than in cats living in forest % by weight) (Fitzgerald & Karl 1979).

In a study area at Te Wharau in the Wairarapa, alysis of cat scats showed that rabbits were the st important prey, especially in the spring when ny young were taken (Gibb et al. 1969). Later in year, the diversity of prey increased. Mice were und in about one-third of the scats, but contributed ly 10–15% by volume, a similar proportion to the sults from Hawke's Bay. Although birds were und less frequently in the scats from Hawke's Bay, ey contributed about the same proportion by weight at Te Wharau. At Kourarau, also in the Wairarapa, ibb et al. (1978) found a higher proportion of bbits (40–100%) than rodents and birds in the scats er 5 years. When rabbits were scarce, caterpillars the *Porina* moth became an important item. Cats ntinued to take adult rabbits throughout the year, d thus kept the density of the enclosed population w. Along the Tekapo River in the MacKenzie asin of the South Island, rabbits were the most equent (86%) prey of cats and rodents and birds ere unimportant (Pierce 1987).

Other studies on the diet of feral cats indicate that bbits are the preferred food. For example, in ictoria, Australia, rabbits were the main food oman & Brunner 1972; Mahood 1980; Jones & oman 1981). In North America the lagomorphs *ylvilagus* spp. and *Lepus* spp. were the staple dietary ems (McMurray & Sperry 1941; Hubbs 1951; Eberhard 1954; George 1974), and in parts of northern Europe (Corbett 1979; Liberg 1984) rabbits were again the main prey.

The paucity of rabbits in the present study area was probably the result of a combination of habitat deficiency and predation. Much of the pasture was too lush to be suitable for rabbits, which prefer short-cropped grass, and other areas were waterlogged for part of the year and unsuitable for burrowing. Both the willows and the windbreaks lacked undergrowth to provide shelter for rabbits living above ground. Many of the areas of boxthorn used previously by rabbits have been removed, and the arable land was regularly planted with different crops, providing little cover. The relatively large populations of cats and ferrets *Mustela putorious furo* were probably sufficient to keep the rabbit population at a very low level (estimated at about 0.05/ha).

Mammals contributed about 93% by weight of the cats' diet in the Orongorongo Valley forest (Fitzgerald & Karl 1979), compared to about 75% in Hawke's Bay. In both studies, rats contributed about 40% of the diet by weight, occurring in about 50% of the scats. Mice were found about as often in the two localities, but in the forest they did not vary seasonally as in the Hawke's Bay farmland, and contributed less by weight overall. In European studies of cat diets in which rodents predominate, cricetids, absent in New Zealand, are preferred almost to the exclusion of rats and mice (Heidemann 1973).

Rats were the most important item of the diet in Hawke's Bay throughout the study, contributing about one-third by weight. The annual increase in number of mice in the scats during autumn and winter was most noticeable in 1984, when mice exceeded rats by weight. In winter, cats switched to scavenging, as suggested for cats in the Orongorongo Valley for the same season (Fitzgerald & Karl 1979). Possums constituted, on average, about 26% by weight in winter compared to about 32% in the valley study. Scavenging was possible only when there were suitable carcasses availabe, and these were provided mainly by bad weather rather than starvation. After this study ended, possums were poisoned with cyanide, and many possum carcasses became available to the cats on the farm. Some carcasses were covered by soil and the scratch marks suggested cats were responsible for making these food caches (P. Herritty, pers. comm.). In the winter of 1985, scavenged possums contributed about 40% by weight of the cats' diet. Over 80% of the possums were found in scats collected near the willows. The ferret was the only other common predator in the area, although the Harrier is also a scavenger of possums, especially road kills.

In Hawke's Bay, birds were important items only in spring and summer, but the preponderance of young birds and the scavenging on larger birds suggests that cats had little effect on their abundance. The relatively stable cat population (2–3/km2) relied on possums and rodents during winter and spring. Young possums did not feature in the cats' diet at Hawke's Bay as they did in the Orongorongo Valley. In this study, the presence of adult possums in the diet depended on environmental factors, such as bad weather and poisoning by man; the cat had no regulatory effect on the population of possums. The impact of cats on the rat population could not be measured. Future studies on the diet of cats in this area will need to monitor the rodent populations and obtain the other information necessary to measure the impact of cat predation on rodents.

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A cladistic analysis of species of the molluscan genus *Potamopyrgus* based on allozyme data*

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Abstract The relationships among four species of the molluscan genus *Potamopyrgus* have been investigated using cellogel electrophoresis. Electrophoretic variability at nine presumptive loci was calculated. Cladograms were constructed using both electromorph and locus as characters. Results indicate two major groupings within the genus. *P. estuarinus* and *P. pupoides* appear to represent sister taxa and, as a grouping, are closely related to *P. antipodarum*. The relationship of *P. troglodytes* to other species of the genus remains problematical. The cladograms obtained are congruent with that based on morphology with respect to *P. antipodarum*, *P. estuarinus*, and *P. pupoides*.

Keywords *Potamopyrgus*; cladistics; electrophoresis; allozymes

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INTRODUCTION

The New Zealand molluscan genus *Potamopyrgus* (Gastropoda: Hydrobiidae) is represented by about four species, although the exact number has been the subject of considerable discussion. For example, Suter (1905) recognised six species and three subspecies of *Potamopyrgus* from the two main islands of New Zealand. In the next major review of the genus, Winterbourn (1970) recognised only three species. The major distinction between these two studies was that Winterbourn recognised the extreme morphological variation within the species *Potamopyrgus antipodarum*, whereas Suter did not.

Since the work of Winterbourn (1970), various taxonomic studies have resulted in addition and subtraction of a number of species from the genus. Climo (1974) recognised a further three species in addition to those described by Winterbourn (1970): *P. cresswelli*, *P. gardneri*, and *P. manneringi*. However, he later placed the latter two species in synomony with the former (Climo 1977). He also transferred *Opacuincola troglodytes* to the genus *Potamopyrgus*, as well as reconstituting the species *P. subterraneus* (recognised originally by Suter 1905). In the most recent review of the genus, Powell (1979) recognised seven species from the main islands, as well as an additional two from outlying islands. Unlike Climo (1974, 1977), Powell (1979) recognised *P. gardneri* and *P. manneringi*; however, he did not include *P. subterraneus* and *P. troglodytes*.

The major criteria used to establish species status in this animal generally incorporate morphological and ecological characteristics (Winterbourn 1970; Powell 1979). However, the extent of morphological variation among the group as a whole is large and distinction of species using these criteria has generally been confused. The extreme morphological variation within *P. antipodarum*, and the similarities observed between certain forms of this species and other species in the genus, suggest that a technique independent of morphological characters might be of use in inferring relationships. Electrophoretic

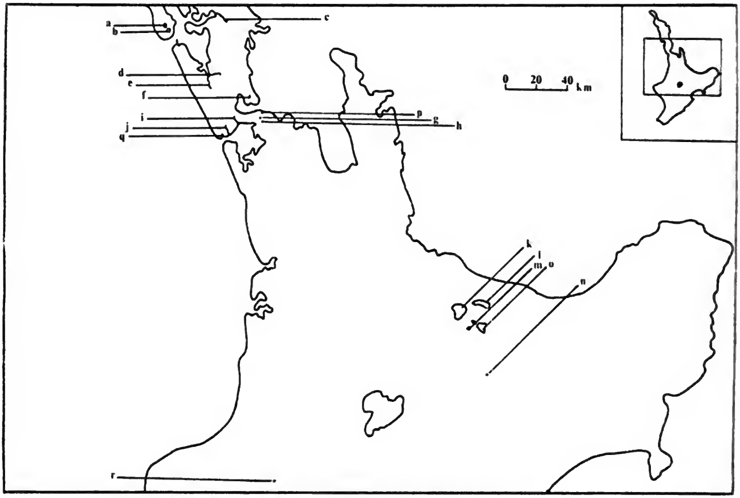


Fig. 1 Collection sites of species of the genus *Potamopyrgus*. a) Lake Rotokawau, b) Lake Kanono, c) Waitangi River, d) Kaukapakapa River, e) Kaipara River, f) Lake Pupuke, g) Domain, h) Cornwall Park, i) Kakamatua Stream, j) Marama Stream, k) Lake Rotorua, l) Lake Rotoiti, m) Green Lake, n) Waiotapu River, o) Lake Tarawera, p) Hobson Bay, q) Huia Dam, r) Aria.

analyses generate a data base that is independent of any morphological study. For this reason an electrophoretic analysis of allozyme characters of four species of the genus *Potamopyrgus* was undertaken. The aim of the study was to construct a phylogenetic classification based on genetic data, this construction being considered important in evaluating the reliability of a phylogeny based only on morphological data, as has been the case previously for this genus, and to estimate congruence of these different data sets.

MATERIALS AND METHODS

Samples of *P. antipodarum*, *P. pupoides*, *P. estuarinus*, and *P. troglodytes* were obtained for electrophoretic analysis from the following sites: *P. antipodarum*—Lake Kanono, Lake Rotokawau, Waitangi River, Kaukapakapa River, Kaipara River, Lake Pupuke, Domain, Cornwall Park, Kakamatua Stream, Marama Stream, Lake Rotorua, Lake Rotoiti, Green Lake, Waiotapu River, Lake Tarawera; *P. estuarinus*—Hobson Bay; *P. pupoides*—Huia Dam; *P. troglodytes*—Aria (Fig. 1). Individuals were prepared for electrophoresis by methods outlined in Phillips & Lambert (1989). For each species 42 specimens were chosen at random from the populations. For *P. antipodarum*, *P. estuarinus*, and *P. pupoides* each sample comprised 21 females and 21 males. Examination of *P. troglodytes* did not produce evidence of males and so the sample was made up of 42 females. In *P. antipodarum* a large number of populations were available and so samples were divided into two geographical regions—Auckland and Rotorua. From within each, 42 individuals were chosen at random. Eleven presumptive loci were screened: GPI-1, GPI-2 (glucose-6-phosphate isomerase), AAT-1, AAT-2 (aspartate aminotransferase), PNP-1 (purine-nucleoside phosphorylase), MDH-1, MDH-2 (malate dehydrogenase), PGD-1 (phosphogluconate dehydrogenase), PGM-1, PGM-2 (phosphoglucomutase), and MPI-1 (mannose-6-phosphate dehydrogenase). Of these, nine were resolved to a consistently scorable level. For the MPI locus only three individuals from each population were examined. Swofford & Berlocher (1987) argue that the use of small or unequal sample sizes is problematic when coding allozyme data as discrete states. Although only three animals were used in MPI, such "limited" sampling still resulted in recognisable differences and was considered suitable for presentation.

To provide polarity in the cladogram construction (Distance Wagner Tree), the gastropod *Physa* sp. was chosen as an outgroup. The use of an outgroup allows for comparison of synapomorphies at one level with those found at a higher level in the hierarchy, thus testing the assumption of monophyly at the lower level (Gaffney 1979). The outgroup must therefore share characters with the ingroup.

RESULTS

Electromorph frequencies are presented in Table 1. These were coded into character/state data following the recommendations of Mickevich & Mitter (1981). Both electromorphs and loci were treated as characters. In the former case (the independent allele model of Mickevich & Mitter 1981), two states—presence or absence—are possible. In the construction of a character/state matrix using electromorphs, a finer-grained approach (employing all electromorphs) (Buth 1984) was employed initially, in which all electromorph frequencies were included (Fig. 2). Construction of the actual matrix involved denoting all electromorphs present as 1 (represented as black squares) and those absent as 0 (represented diagrammatically as white squares), thus producing a binary system representing frequency data. A coarser grained approach, in which a minimum allele frequency of 0.05 or greater was necessary for coding as "present", was also employed, being constructed in a similar manner (Fig. 3).

When the locus was treated as the character, two matrices were also generated. The character state in each instance was defined by a particular electromorph combination denoting that locus, with only the more commonly occurring electromorphs (frequency greater than or equal to 5%) being included. For example, at the GPI-1 locus the presence of the combination 105/100 was designated character A, 110 as state B, and 150 as state C. For each new locus, character states were redefined. In this way, character states for *P. antipodarum* were always designated as A and all others were relative to this (the choice of this species, as the point from which all others were designated, was arbitrary). From this, a simple unordered presence/absence matrix using alphabetical designation was generated. This matrix was then transformed either (A) into binary numbers (as for the electromorph-as-character matrices), producing a finely grained matrix (Fig. 4) or (B) into integer form, producing a coarser grained matrix (Fig. 5). This latter transformation involved designating the first character state at each locus in the matrix generated from transformation (A) as 1, with all other states being defined in relation to this. Hence, for the GPI-1 locus, the binary representation of *P. antipodarum* is 100 and the corresponding numerical state is 1. For transformation (B) the state present is represented by a particular coloured square, rather than in integer form. Once in the appropriate form, the data were analysed for genetic relatedness between species using PAUP Version 2.4 (Swofford 1985), resulting in the construction of rooted trees (cladograms). In this programme, a "branch and bound" method (similar to that employed by Hendy & Penny 1982) using a Wagner algorithm is applied to the data, the result being that all most parsimonious trees (i.e., those of minimal length) are found. To provide polarity in the construction of the Wagner tree, an outgroup was used (see above).

When all electromorph frequencies were included in the character/state matrix (fine-grained approach) three equally parsimonious cladograms were generated (Consistency Index CI=0.812) (Fig. 2), while the coarser-grained approach (electromorph frequency ≥ 0.05) yielded a single tree, this being identical to one of the three trees initially generated, although slightly more parsimonious (Consistency Index CI=0.833) (Fig. 3).

When the locus was used as the character both matrices produced identical cladograms, although from the integer matrix a more parsimonious cladogram was obtained (CI= 1.00) (Fig. 4, 5). Such a result is not surprising as the same data were employed in both instances. The tree obtained was identical to one of the trees produced when all electromorphs were included as characters (no cutoff point).

DISCUSSION

The cladograms generated using electromorphs and loci as characters indicate two groupings in this genus. In all trees constructed it is clear that *P.*

pupoides and *P. estuarinus* are sister taxa and, as the group *estuarinus-pupoides*, are sister taxa to *P. antipodarum*. The phylogenetic relationship of *P. troglodytes* to the other species is less obvious as its position in the cladogram varies considerably. The most parsimonious tree (Fig. 5) suggests that *P. troglodytes* would be a sister taxon to the *P. estuarinus-pupoides* group, rather than to *P . antipodarum*.

The use of *Physa* sp. as an outgroup is problematical. Examination of Table 1 shows that six of the nine loci are uninformative in that they share no allelic products with the ingroup. Of the three loci that are shared and therefore informative, PNP-1 shows only an autapomorphic condition for *pupoides* and MDH-1 and MDH-2 show synapomorphies for *pupoides* and *esturarinus*. Nevertheless the nine loci are sufficient for resolving

Table 1 Electromorph frequencies at nine presumptive loci in four species of *Potamopyrgus* & one of *Physa* sp.

			Taxa					
Locus	Sample size	Electromorph	*antipodarum*–1 (Auckland)	*antipodarum*–2 (Rotorua)	*pupoides*	*estuarinus*	*troglodytes*	*Physa* sp
AAT–1	42	85	–	–	–	–	–	1.000
		95	–	0.024	–	–	–	–
		97	–	–	–	1.000	1.000	–
		100	1.000	0.976	–	–	–	–
		110	–	–	0.500	–	–	
		115	–	–	0.500	–	–	–
GPI–1	42	100	0.974	0.837	–	–	0.590	–
		105	0.007	0.153	–	0.708	0.410	–
		110	0.005	0.002	0.706	0.292	–	–
		115	–	0.002	0.294	–	–	–
		125	0.007	0.002	–	–	–	–
		130	0.005	0.002	–	–	–	–
		135	0.002	0.002	–	–	–	–
		150	–	–	–	–	–	1.000
MDH–1	42	90	–	–	1.000	1.000	–	–
		100	1.000	1.000	–	–	0.500	0.550
		105	–	–	–	–	0.500	0.450
MDH–2	42	90		–	0.500	1.000	–	–
		95	–	–	0.500	–	–	–
		100	1.000	1.000	–	–	0.500	1.000
		105	–	–	–	–	0.500	–
MPI–1	3	100	1.000	1.000	1.000	1.000	1.000	–
		110	–	–	–	–	–	1.000
PGD–1	42	100	1.000	1.000	–	1.000	1.000	–
		105	–	–	1.000	–	–	–
		110	–	–	–	–	–	1.000
PGM–1	42	95	0.928	0.933	–	–	0.500	–
		100	–	–	–	–	0.500	–
		105	0.072	0.067	–	–	–	–
		140	–	–	–	–	–	1.000
PGM–2	42	95	0.928	0.934	0.500	0.375	0.500	–
		100	–	–	0.500	0.625	0.500	–
		105	0.072	0.066	–	–	–	–
		130	–	–	–	–	–	0.500
		135	–	–	–	–	–	0.500
PNP–1	42	100	0.843	0.880	–	0.500	0.500	1.000
		105	0.157	0.120	–	–	–	–
		110	–	–	–	0.500	0.500	–
		115	–	–	0.500	–	–	–
		120	–	–	0.500	–	–	–

LOCUS	AAT-1						GPI-1								MDH-1			MDH-2				MPI-1		PGD-1			PGM-1				PGM-2					PNP-1				
ELECTROMORPH	A	B	D	E	K	N	A	C	D	E	G	H	I	M	A	C	F	A	B	C	F	A	D	A	C	D	A	B	C	L	A	B	C	H	I	A	B	C	D	E
SPECIES																																								
ANT-1	■	□	□	□	□	□	■	■	■	□	■	■	■	□	■	□	□	■	□	□	□	■	□	■	□	□	■	□	■	□	■	□	■	□	□	■	■	□	□	□
ANT-2	■	■	□	□	□	□	■	■	■	■	■	■	■	□	■	□	□	■	□	□	□	■	□	■	□	□	■	□	■	□	■	□	■	□	□	■	■	□	□	□
PUP	□	□	■	■	□	□	□	□	■	■	□	□	□	□	□	□	■	□	■	□	■	■	□	□	■	□	□	□	□	□	■	■	□	□	□	□	□	□	■	■
EST	□	□	□	□	■	□	□	■	■	□	□	□	□	□	□	□	■	□	□	□	■	■	□	■	□	□	□	□	□	□	■	■	□	□	□	■	□	■	□	□
TROG	□	□	□	□	■	□	■	■	□	□	□	□	□	□	■	■	□	■	□	■	□	■	□	■	□	□	■	■	□	□	■	■	□	□	□	■	□	■	□	□
PHYS	□	□	□	□	□	■	□	□	□	□	□	□	□	■	■	■	□	■	□	□	□	□	■	□	□	■	□	□	□	■	□	□	□	■	■	■	□	□	□	□

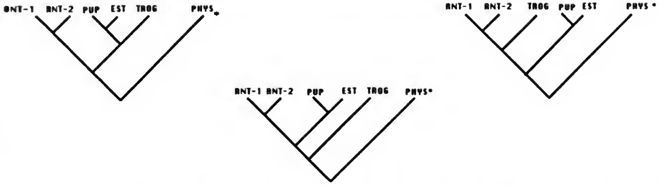


Fig. 2 Presence (black squares) / absence (white squares) matrix and corresponding cladograms generated when electromorph is used as character (no cutoff point), * designates the outgroup [ANT-1 = *P. antipodarum* (Auckland), ANT-2 = *P. antipodarum* (Rotorua), PUP = *P. pupoides*, EST = *P. estuarinus*, TROG = *P. troglodytes*, PHYS = *Physa* sp.]

LOCUS	AAT-1					GPI-1					MDH-1			MDH-2				MPI-1		PGD-1			PGM-1			PGM-2					PNP-1				
ELECTROMORPH	A	D	E	K	N	A	C	D	E	M	A	C	F	A	B	C	F	A	D	A	C	D	A	C	L	A	B	C	H	I	A	B	C	E	D
SPECIES																																			
ANT-1	■	□	□	□	□	■	□	□	□	□	■	□	□	■	□	□	□	■	□	■	□	□	■	□	□	■	□	■	□	□	■	■	□	□	□
ANT-2	■	□	□	□	□	■	■	□	□	□	■	□	□	■	□	□	□	■	□	■	□	□	■	□	□	■	□	■	□	□	■	■	□	□	□
PUP	□	■	■	□	□	□	□	■	■	□	□	□	■	□	■	□	■	■	□	□	■	□	□	□	□	■	■	□	□	□	□	□	□	■	■
EST	□	□	□	■	□	□	■	■	□	□	□	□	■	□	□	□	■	■	□	■	□	□	□	□	□	■	■	□	□	□	■	□	■	□	□
TROG	□	□	□	■	□	■	■	□	□	□	■	■	□	■	□	■	□	■	□	■	□	□	■	■	□	■	■	□	□	□	■	□	■	□	□
PHYS	□	□	□	□	■	□	□	□	□	■	■	■	□	■	□	□	□	□	■	□	□	■	□	□	■	□	□	□	■	■	■	□	□	□	□

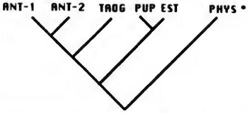
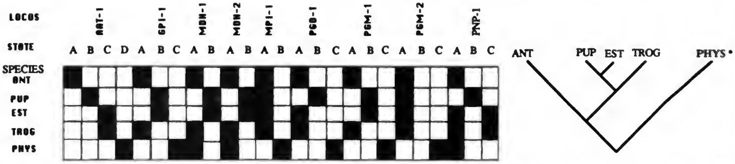
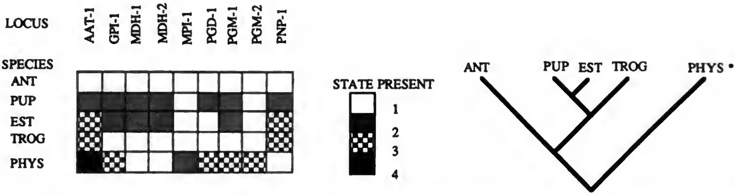


Fig. 3 Presence (black squares) / absence (white squares) matrix and corresponding cladogram generated when electromorph is used as character (electromorph frequencies ≥ 0.05), * designates the outgroup [ANT-1 = *P. antipodarum* (Auckland), ANT-2 = *P. antipodarum* (Rotorua), PUP = *P. pupoides*, EST = *P. estuarinus*, TROG = *P. troglodytes*, PHYS = *Physa* sp.]



LOCUS	AAT-1				GPI-1			MDH-1		MDH-2		MPI-1		PGD-1			PGM-1			PGM-2			PNP-1		
STATE	A	B	C	D	A	B	C	A	B	A	B	A	B	A	B	C	A	B	C	A	B	C	A	B	C
SPECIES ANT	■	□	□	□	■	□	□	■	□	■	□	■	□	■	□	□	■	□	□	■	□	□	■	□	□
PUP	□	■	□	□	□	■	□	□	■	□	■	■	□	□	■	□	□	■	□	■	□	□	□	■	□
EST	□	□	■	□	□	■	□	□	■	□	■	■	□	■	□	□	□	■	□	■	□	□	■	□	■
TROG	□	□	■	□	■	□	□	■	□	■	□	■	□	■	□	□	■	□	□	■	□	□	■	□	■
PHYS	□	□	□	■	□	□	■	■	□	■	□	□	■	□	□	■	□	□	■	□	□	■	■	□	□

Fig. 4 Presence (black squares) / absence (white squares) and corresponding cladogram generated when locus used as character (unordered matrix, fine-grained approach employing binary numbers).* designates the outgroup [ANT-1 = *P. antipodarum* (Auckland), ANT-2 = *P. antipodarum* (Rotorua), PUP = *P. pupoides*, EST = *P. estuarinus*, TROG = *P. troglodytes*, PHYS = *Physa* sp.]



LOCUS	AAT-1	GPI-1	MDH-1	MDH-2	MPI-1	PGD-1	PGM-1	PGM-2	PNP-1
SPECIES ANT	□	□	□	□	□	□	□	□	□
PUP	▓	▓	▓	▓	□	▓	▓	□	▓
EST	▦	▓	▓	▓	□	□	▓	□	▦
TROG	▦	□	□	□	□	□	□	□	▦
PHYS	■	▦	□	□	▓	▦	▦	▦	□

STATE PRESENT
□ 1
▓ 2
▦ 3
■ 4

Fig. 5 Matrix of character states present and corresponding cladogram generated when locus is used as character (unordered matrix, coarse-grained approach employing integers).* designates the outgroup [ANT-1 = *P. antipodarum* (Auckland), ANT-2 = *P. antipodarum* (Rotorua), PUP = *P. pupoides*, EST = *P. estuarinus*, TROG = *P. troglodytes*, PHYS = *Physa* sp.]

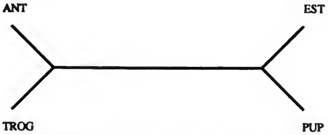


Fig. 6 Cladogram generated when outgroup is removed from the analyses.

the relationships of the ingroup. If we remove the outgroup from the cladograms the same relationship always appears (Fig. 6). It should be noted that this relationship is not inconsistent with that generated from the rooted networks.

The questionable taxonomic status *P. troglodytes* found in this study is not surprising, if the following is considered. Firstly, Climo (1977) transferred *Opacuincola troglodytes* to the genus *Potamopyrgus* on the basis of morphological similarities with members of this genus. His original classification of *O. troglodytes* was based on shells from a single location. Secondly, Powell (1979) did not recognise Climo's classification, and, in fact, suggested that *O. troglodytes* was barely distinguishable from *O. caeca* (the major difference being the smaller size of the former).

The direct phylogenetic analysis of electromorphs as character avoids the information loss that attends reducing character data to distances, as is generally done when using a phenetic approach (Farris 1981). The classification generated is dependent upon whether the electromorph or locus is used as character. The former approach is supported by, for example, Mickevich & Mitter (1981), whereas Buth (1984) prefers the latter. The production of a single more parsimonious tree in this study, using loci as characters, would appear to support the latter approach.

The results obtained in this study indicate two major groupings in the genus *Potamopyrgus*. The set of relationships found in this study confirms those suggested by Winterbourn (1970) based on overall morphological similarity of the species *antipodarum*, *estuarinus*, and *pupoides*. The relationship of *P. troglodytes* to the other species is less obvious and the reliability of its classification based on morphological characters cannot be evaluated using the phylogenetic classification. It can, however, be concluded that the cladograms based on electrophoretic data in this study are congruent with that based on morphology for the species *antipodarum*, *estuarinus*, and *pupoides*.

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ionicola (Pentatax) billieaehonore n. sp. a sponge-associated dracarina (Acari: Unionicolidae) from New Zealand

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stract Records of sponge-associated Iracarina from the Southern Hemisphere are ommon. *Unionicola (Pentatax) billieaehonore* p. has been found in association with the fresh- er sponge *Ephydatia kakahuensis* in Lake Rotoiti rth Island) and Lake Taupo in New Zealand. ferences in palpal characteristics and in setal terns of the epimera distinguish this species from holotype of *Unionicola longiseta* Walter 1915 ich was reported from New Zealand by Schröder 35).

ywords *Unionicola billieaehonore* n. sp.; dracarina; Acari; Unionicolidae; freshwater nge

TRODUCTION

e water mites, or Hydracarina, developmentally ociated with freshwater sponges in the Northern misphere are a complex of seven species tributed as follows: *Unionicola crassipes* (Muller 76) and *U. minor* (Soar 1900) in Europe (Hevers 75 1977 1978); *U. nearctica* Crowell & Davids 79 and *U. laurentiana* Crowell & Davids 1979 in rth America; *U. miyazaki* Imamura 1953 and *U. gata* Imamura 1954 are found in Japan (Hevers 84); and *U. crassipes*, *U. miyazaki*, and *U. gilani* vers 1984 in Iran (Hevers 1984). Reports of *U. crassipes* outside the stated range have not been associated with freshwater sponges and in certain instances the records remain in need of verification. Reports of sponge-associated water mites from the Southern Hemisphere are very limited. Schröder (1935), in reviewing the biology of freshwater sponges in New Zealand, Borneo, and Madagascar, reported two mite specimens from sponges growing on the shells of living and dead mussels (*Hyridella menziesi*) taken in Lake Waikare in New Zealand. Those mites were identified as *Unionicola (Pentatax) longiseta* Walter 1915. In a review of the relationships between mites and sponges, Arndt & Viets (1938) included a listing of *U. (Pentatax) affinis* (Piersig) collected by an exploratory expedition in Stan-See, Tjigonborg, Buitenzorg (Indonesia). This paper is based on a study of the sponge-associated mites in New Zealand in an attempt to clarify the identity of that fauna.

MATERIALS AND METHODS

From February through July 1984 and January and February 1987, extensive field collections were made on both the North and South Islands of New Zealand. Repeated attempts to collect sponges in Lake Waikare, Schröder's reported locality, were unproductive. That lake has become highly dystrophic over recent years according to ecologists familiar with it.

Sponge-associated *Unionicola* were collected in Lake Rotoiti (North Island) and in Lake Taupo. Additional specimens of *Unionicola* were provided by Dr Ceri Hopkins from collections made in the Kaikoka Lakes on South Island. Collections include adults and developmental stages found in the sponge *Ephydatia kakahuensis*.

Mites were collected primarily by means of light traps constructed of metal cans with plastic funnels and equipped with Cyalume chemical light sticks. Traps were generally left in place over night.

Specimens were either killed and fixed in Koenike's fluid for subsequent slide mounting or fast-frozen over dry ice (CO2) and dehydrated in

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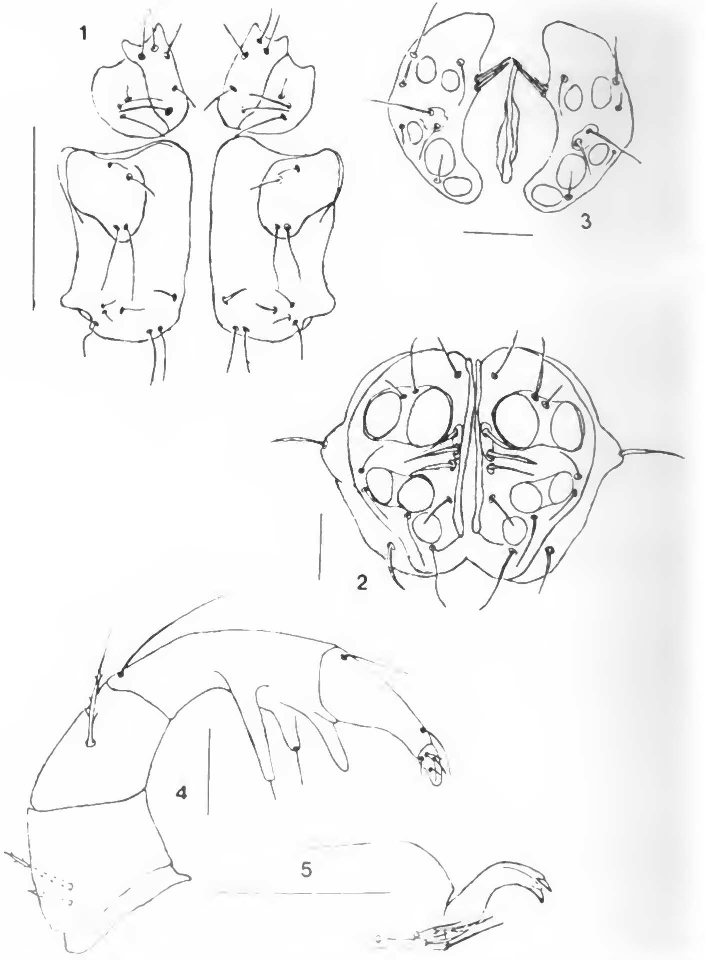

Fig. 1–5 *Unionicola billieaehonore*, n. sp.; 1. Epimera. (female); 2. External genitalia. (female); 3. External genitalia (male); 4. Right palp, lateral view. (female); 5. Pre-tarsus, leg I. Scale lines equal 50 µm.

tone for examination by scanning electron roscopy. Drawings were prepared from SEM tographs. The instrument used is a model ISI-IA in the St Lawrence University Departments of logy and Geology provided under NSF Grant 8166220 to Crowell and Erickson.

It was originally thought that the specimens of s study represent the species collected by Schröder. wever, a comparison of them with the type material *Unionicola longiseta* deposited by Walter in the turhistorisches Museum in Basel, Switzerland, ws certain differences which warrant their scription as a distinct species.

ionicola (Pentatax) billieaehonore n. sp.

agnosis. Unionicolids with characteristics of the nus *Unionicola* and the subgenus *Pentatax*. males averaging 680 µm(range 580–730 µm) in gth; males 640 µm (range 570–730 µm). Palps 7 µm; fused coxae III + IV > 1.5× longer than de.

Unionicola billieaehonore is a small mite, notably aller than most other members of the subgenus own from the Australian region.

The epimera of this mite are characteristic in pe as are their setal patterns (Fig. 1). The first imera bear five pairs of setae, three anteriorly, one r near the medial margin about two-thirds the imeral length from its anterior tip, and one posterior r near the lateral margins of the epimera. Epimera bear three pairs of setae near the center of the imeral plate, the middle seta being slightly lateral a line joining the other two.

Fused epimera III + IV of this species are distinctly portioned being greater than 1.5× longer than de. Epimera III bear two relatively short, fine ae situated near the anterior-medial boundary of h epimeron III and two longer, stouter setae ated near the posterior-medial corner. Epimera bear three very fine setae clustered just medially the point of attachment of the fourth leg, four nger and stouter setae are located along the sterior-medial boundary of the epimeron, one jacent to the base of the fourth leg, two near the sterior-medial corner of the epimera, and one istle-like setae just anterior to those.

The external genitalia of females (Fig. 2) consists two pairs of acetabular plates, the anterior pair ing only indistinctly separated from the posterior ir. The anterior genital plates each bear two ominent acetabula; the posterior plates each bear ree acetabula. Flanking the genital orifice are three pairs of long, stout bristle-like setae and posterior to them a single pair of slightly smaller setae. Two setae are situated between the anterior acetabula on each plate and another near the anterior-medial border of each plate. Two other setae are located on each genital plate just behind each of the two most posterior acetabula. Laterally, just off the genital plates and arising from prominent glandular humps are a pair of stout, long setae, and another prominent pair of setae near the posterior-lateral margin of the plates.

A pair of semilunate acetabular plates (Fig. 3) form the external male genitalia. The acetabula, comprising of two pairs anteriorly and three pairs posteriorly, are distinctly smaller than those of females. Two pairs of long, stout setae flank the genital orifice about one-third of the plate length from the anterior tip. Three pairs of setae are associated with the two anterior acetabula, one pair medially situated and two pairs laterally. A pair of irregular, slightly-raised plates is located just anterior to the posterior cluster of acetabula. Each of these small plates bears two apparently glandular setae set in prominent depressions. Smaller setae, two pairs, flank the three posterior acetabula on each plate.

The palps of a representative *U. billieaehonore* female (Fig. 4) are 377 µm in length, exclusive of the pretarsus, with individual segments as follows: trochanter (P–I) 10 µm; femur (P–II) 65 µm; genu (P–III) 76 µm; tibia (P–IV) 130 µm; and tarsus (P–V) 90 µm.

The palpal tibia (P–IV), the longest and slenderest of the podomeres, bears on its flexor surface three prominent tooth-like pegs. The lateral and longest of these is about 1.7× the dorso-ventral dimension of the podomere where the peg arises. The palpal tibia (P–IV) is also distinctive in being 2× the length of P–II, the palpal femur.

The palpal femur (P–II) bears two feathered setae on its medial surface and P–III bears one such seta on its lateral surface. Long, simple setae are borne on the extensor surface of P–IV and P–V near their respective proximal ends, and one such on the distal end of P–V. Similar simple setae are apparent on the tip of two of the three pegs on P–IV. The palpal pretarsus forms a double claw-like tip with four associated sensory setae.

The pretarsus of the first leg of this species is a double claw (Fig. 5). Each claw is shown under SEM examination to be bifurcate at its tip. The claw is highly arched and its total length is about equal to the height of the tarsal segment. A cluster of five stout setae is present near the tip of the tarsus.

Type Material. Holotype, allotype, and paratypes of *Unionicola (Pentatax) billieaehonore* n. sp. will be deposited in DSIR Plant Protection, Mt Albert Research Centre, Auckland, New Zealand. Paratypes will be deposited in the Naturhistorisches Museum in Basle, Switzerland and in the Royal Ontario Museum, Toronto, Ontario, Canada.

Etymology. This species is named in appreciation and gratitude to my wife, Billie, for many years of assistance in field collections, seemingly interminable hours of searching for and sorting water mites, and general support of my research and professional activities.

COMPARISONS

Unionicola (Pentatax) billieaehonore is distinct from other members of this subgenus occurring in the Australian region in size, epimeral proportions, setal patterns, characteristics of the palps, the external genitalia, and the first pretarsus.

The presence of pegs on the flexor surface of P–IV in *U. billieaehonore* distinguishes it from the six species described by Viets (1980): *U. walkeri, U. procursa, U. conjunctella, U. liqulifera, U. clipeata,* and *U. scutata*; and from *U. crassitpalpis* Walter 1915. The six Australian species of Viets (1980) were collected from mussels.

The same characteristics Walter (1915, p. 101) used to separate *U. necessaria* (Koenike) and *U. longiseta* Walter, namely the size and position of the eyes, and of the glands of Claparede, distinguish *U. billieaehonore* and *U. necessaria*.

A modern description of *U. affinis* (Piersig) by Cook (1967, p. 122) will separate that confusing taxon from *U. billieaehonore*. In *U. affinis* the fused epimera III + IV are only 1.2× longer than wide compared to 1.5× longer than wide in *U. billieaehonore*. Likewise P–IV (palpal tibia) is only 1.1× the length of P–II (palpal femur) in *U. affinis* compared to 2× in *U. billieaehonore*. (See Walter 1929, fig. 13.) *U. affinis* has been recorded from sponges in Java. (Arndt & Viets 1938).

Walter (1915) compares his *U. longiseta* as similar to the European species *U. figuralis* (Koch, 1836): "...et montre plus de grandes affinites avec *Unionicola figuralis*... de l'Europe." Using a very precise set of measurements and figures by Hevers (1975, Pl. 21, 22, 42) *U. figuralis* and *U. bilieaehonore* can be separated by comparing proportions of the coxal plates III + IV and palpal segments II and IV.

Specimens of *U. figuralis* in the collection of C. Davids at the University of Amsterdam were also examined for comparison of palpal segments P–II and P–IV. In 15 palps the palpal femur, P–II, averaged 1.06× longer than P–IV (range 0.95×–1.32×). (Measurements made by C. de Groot and provided by C. Davids, pers. comm.). These data confirm the difference of the palps of *U. figuralis* and *U. billieaehonore*.

U. figuralis has been reported from mollusks (Viets & Plate 1954).

This new species is distinct from *U. longiseta*, likely its nearest relative, in a number of characteristics. Notable is the small size of *U. billieaehonore*. Its maximum length of 730 µm is only 0.87 of the minimum length of 830 µm reported by Walter. The mean length, 635 µm, of *U. billieaehonore* is 0.7 of the 900 µm for "most" specimens examined by Walter. Likewise, the mean width of specimens of *U. billieaehonore*, 484 µm (430–620 µm), is about 0.7× the width of 720 µm recorded by Walter for *U. longiseta*. The mite described by Lundblad (1941) as *U. australica* and later (Lundblad 1947) synonymised with *U. longiseta* is a smaller mite than those of the New Caledonia population, but other morphological traits distinguish *U. billieaehonore* from that population.

The fused epimera III + IV in *U. billieaehonore* are at least 1.5× longer than wide compared to 1.2× longer than wide in the holotype of *U. longiseta*.

Epimera I of *U. billieaehonore* possesses two prominent setae near its posterior border which are lacking in *U. longiseta*. Similarly, epimeron IV of the new species bears three prominent setae near its posterior medial corner not present in *U. longiseta*.

The external genitalia of female mites has a greater number of stout setae on the posterior ends of the acetabular plates in *U. billieaehonore* than in *U. longiseta*. The male acetabular plates of *U. billieaehonore* exhibit two prominent pairs of stout setae midway on the plate associated with glandular bases, an arrangement not apparent in males of *U. longiseta*.

The greater proportionate length of the palpal tibia (P–IV) in *U. billieaehonore*, where it is 2× the length of the palpal femur (P–II), differs from *U. longiseta* where P–II is equivalent to or slightly longer than P–IV (1.05–1.11). In *U. billieaehonore* the lateral peg on the palpal tibia is 1.7× the dorsoventral dimension of the segment at its point of attachment, whereas in *U. longiseta* it is 1.35× the thickness of the podomere.

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The New Zealand species of *Stethorus* Weise (Coleoptera: Coccinellidae)

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Abstract Adults of the three New Zealand *Stethorus* species—*S. bifidus* Kapur, *S. griseus* Chazeau, and *S. histrio* Chazeau—are redescribed and keyed. Short descriptions of the last instar-larvae of *S. bifidus* and *S. griseus* are provided. Notes on nomenclature, affinities, distributions, and hosts are presented and a lectotype designated for *S. griseus*. *S. griseus* Whitehead and *S. incompletus* Whitehead are nomina nuda and *S. incompletus* Chazeau is treated as a synonym of *S. histrio*. The record of the Australian species *S. nigripes* Kapur from New Zealand is incorrect.

Keywords Coleoptera; Coccinellidae; *Stethorus bifidus*; *S. griseus*; *S. histrio*; taxonomy

INTRODUCTION

Kapur (1948) described *Stethorus bifidus* from New Zealand. In an unpublished thesis, Whitehead (1967a) described *S. griseus* and *S. incompletus*. Chazeau (1979) used both these unavailable names in a key to Oceanian *Stethorus* species, making them available from that date. However, *S. incompletus* is a synonym of *S. histrio* Chazeau. This study was made to provide a full description for *S. griseus* and to clarify the nomenclature and species present in New Zealand. Some available larval material allowed short descriptions of the last instar larva of *S. griseus* and *S. bifidus*.

In specimen lists only examined localities are given, except for type material, those with associated adults and larvae, incorrect locality or identifiable prey, those whose larval or egg colour was noted, and specimens either from the T. Broun and A. E. Brookes Collections, or collected before 1940; data for such material is given in full. I accepted that the common name of CRM (citrus red mite) referred to *Panonychus citri* (McGregor), European red mite to *P. ulmi* (Koch), twospotted [mite] to *Tetranychus urticae* Koch, and that *T. telarius* L. is a synonym of *T. urticae*. The prey records of red mite, red spider, or spider eggs etc. could not be reliably attributed to a particular species. Area codes are those of Crosby et al. (1976). Some pinned material (including types) of E. Collyer from the Nelson area was incorrectly labelled by V. B. Whitehead as Wellington (J. C. Watt, pers. comm. 1984) and this is noted where appropriate. Information additional to that on labels is enclosed in square brackets. Any number(s) in parentheses after a range of numbers is that most commonly found. All specimens are in NZAC except where indicated.The following abbreviations are used for institutions: AMNZ, Auckland Institute and Museum, Auckland; BMNH, British Museum (Natural History), London; FRNZ, Forest Research Institute, Rotorua; LCNZ, Lincoln College, Canterbury; NZAC, New Zealand Arthropod Collection, DSIR, Auckland; QDPI, Queensland Department of Primary Industries, Brisbane.

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KEY TO THE NEW ZEALAND SPECIES OF *STETHORUS* WEISE

1. Elytra with long sparse semi-erect pubesence, punctures deeply impressed; metasternum distinctly convex posteromedially, with large deep punctures laterally but smaller and shallower posteromedially; femoral line complete and extending to three-quarters or more length of abdominal sternite 1, area within femoral line and lateral metasternum smooth or lightly reticulate .... *bifidus*

   Elytra with short dense pubescence, punctures moderately to shallowly impressed; metasternum relatively flat posteromedially, with small or shallow punctures laterally; femoral line of abdominal sternite 1 complete or incomplete, area within femoral line and lateral metasternum densely reticulate 2

2. Elytral pubescence semi-erect in anterior half and decumbent posteriorly, punctures moderately impressed; metasternum with small deep punctures including posteromedially; femoral line usually complete, extending to about two-thirds length of abdominal sternite 1 .... *griseus*

   Elytral pubescence decumbent, punctures shallowly impressed; metasternum with shallow punctures particularly posteromedially; femoral line incomplete, extending to three-quarters or more length of abdominal sternite 1 .... *histrio*

Stethorus griseus Chazeau

(Fig. 1–7)

Stethorus griseus Whitehead, 1967a: 179, 1967b: 1565. Nomen nudum.

Stethorus griseus Chazeau, 1979: 300; Gordon & Chapin, 1983: 234.

Adult

Coloration. Body black to brown, often lighter on hypomera, epipleurae, and abdominal sternites 5, 6; antennae yellow; mouthparts brown, sometimes yellow; legs dark to light brown with tibiae and tarsi lighter and often yellow, trochanters and forelegs sometimes yellow.

Body. Length 1.09–1.29 mm, width 0.76–0.85 mm. Elytra with short dense pubescence, semi-erect in anterior half, decumbent posteriorly; punctures small, moderately shallow and close. Metasternum and abdominal sternite 1 with small, deep, and close punctures but shallower posteriorly on sternite 1, reticulate laterally; metasternum flat to slightly convex medially. Femoral line complete, extending about two-thirds distance between hind coxa and posterior margin of abdominal sternite 1, rarely narrowly incomplete; area within femoral line mostly reticulate with small shallow punctures. Apex of abdominal sternite 6 rounded in both sexes.

Male genitalia. Sipho (Fig. 1) S-shaped with a notch beside small, often partly unpigmented capsule; distal quarter to fifth with many fine setae and dorsal side unpigmented; with apical and preapical pores. Trabes shallowly concave or straight proximally in dorsal view (Fig. 2). Basal piece wider than long and longer than deep, proximally bilobed with greatest depth. Median lobe extending to or slightly beyond apex of parameres; cone-shaped in dorsal view (Fig. 2), length about 2 times width; tongue-like in lateral view (Fig. 3) with apex downturned. Parameres with setae and pores ventrally and apically, (Fig. 4, 5)

Female genitalia. Genital plates (Fig. 6) with posterolateral margin partly to completely pigmented, with pores in apical half and 0–5 (1) setae at apex. Spermatheca (Fig. 7) annulate and C-shaped.

Last instar larva

Unpigmented. Mouthparts similar to those of *S. fenestralis* Houston (Houston 1980) except for slight differences in length of setae and palps. Maxillary and labial palps less than twice as long as wide; posterior setal pair on mentum-submentum usually not reaching base of median pair (as in fig. 14 for *S. fenestralis* in Houston 1980). Each tibiotarsus with about 16 clavate apical setae, including 1 pair of long thick dorsal setae with remaining setae distinctly shorter proximally but becoming progressively longer distally.

Type data. Lectotype (here designated), Dun Track, Nelson, 19 Feb 1966, E. Collyer; another white label "*Stethorus griseus* Whitehead 72", and a red label "*Stethorus griseus* TYPE V.B.W. 72". Paralectotypes: 4, same data as holotype; 13, Dun Track, [Nelson], Feb 1967, E. Collyer; 1 *S. griseus* and 1 *S. histrio*, Stanton's citrus, [Nelson], Nov 1966, E. Collyer, *Panonychus citri*, dark eggs; 1, Nelson [incorrectly labelled as Wellington], 1965, E. Collyer, mites on apple; 5, Totaranui, Mar 1967, E. Collyer, *Tetranychus urticae*; all also with another white label "*Stethorus griseus* Whitehead 72", and an orange label "Paratype V.B.W. 72".

Adult material examined. New Zealand. 2 (paratypes of *S. bifidus*); T. Broun and A. E. Brookes lections, 2; 13 Jan ?2, spider eggs on *Prunus* ıestica L., 10. RTH ISLAND. **ND**. Kauri Sanctuary, Omahuta :e Forest, 1; Coppermine I, Chickens Is, 2. **AK**. uhoropapa I, Noises Is, 1; Otata I, Noises Is, 2; :kland, 4; Howick, T. Broun and A. E. Brookes lections, 2. **CL**. Stanley I, Mercury Is, 1; Tapu - summit, 1; Tapu Saddle, Coromandel, 1. **BP**. :gerald Glade, [near Tapapa], 1. **GB**. Gisborne, 3. . Paiaka, 12. **RI**. Mangaweka Hills, 1, (AMNZ); ara Reserve, Pohangina Valley, 1. **WI**. Palmerston rth, 26 Nov 1936, W. Cottier, predacious on *Tet- ychus urticae* on *Phormium tenax*, 18; Foxton, 5. UTH ISLAND. **SD**. Te Mahia, 27 Mar 1967, *cesteria*, dark larvae, 14; Te Mahia, 27 Apr 1967, cesteria, pale larvae, 1; Te Mahia, 27 Apr 1967, Collyer, pale larvae, 1. **NN**. Totaranui, Mar 1967, cesteria, dark larvae, 6; Totaranui, Mar 1967, *ranychus urticae* on *Leycesteria*, 16; Astrolabe, aio, 15 Jan 1966, 2; Nelson, 19; Dun Track, lson, 19 Feb 1966, *Tetranychus urticae* on *cesteria*, 29; Dun Track, Nelson, 10 Feb 1967, E. llyer, 1 (paratype of *S. incompletus*); Dun Track, lson, 10 Feb 1967, feeding on *Tetranychus urticae*, e larvae, 2; Perry's orchard, [Nelson], Jan 1967, k larvae, 4; **MB**. Hamner, 1. **KA**. Wairiri, Kaiura, T. Broun and A. E. Brookes Collections, 1. . Granville Forest Camp 19 [near Totara Flat], 1, NZ). **NC**. Omihi State Forest, 8, (FRNZ); Lees lley near Oxford, Canterbury, 1, (FRNZ); Alford te Forest, 1, (FRNZ). **MC**. Christchurch, 2, NZ); Riccarton Bush, Christchurch, 15 Sep 1936, S. Gourley, 1; Lincoln College [Christchurch], 25 t 1961, R. A. Harrison, ex *Tetranychus urticae* ony, 1, (LCNZ); Ardagh [=Methven], 14 Feb 12, T. Broun and A. E. Brookes Collections, 1; thven, 1 Aug 1912, T. Broun and A. E. Brookes llections, 1. **OL**. Makarora, 3, **CO**. Alexandra, 1.

rval material examined. New Zealand. 13 Jan? spider eggs on *Prunus domestica* L. **NN**. Astrolabe, aio, 15 Jan 1966, 1 on slide; Dun Track, Nelson, Feb 1966, *Tetranychus urticae* on *Leycesteria*, so with *S. bifidus* larvae).

marks. The male and female genitalia of *S. iseus* are very similar to those of the Australian *S. gripes* Kapur, except that the sipho is S-shaped th hairs distally. This is the only *Stethorus* species th a row of setae on the sipho.

ethorus bifidus Kapur

ig. 8–11)

Scymmus sp. Cottier, 1934: 68 (larva).
Stethorus bifidus Kapur, 1948: 317; Whitehead, 1967a: 180; Chazeau, 1979: 296; Gordon & Chapin, 1983: 234.
Stethorus bifidus: Bielawski, 1976:393 [misident. for *S. vagans* (Blackburn)].

Adult

Coloration. Body black to brown; hypomera, epipleurae, and abdominal sternites lighter; antennae yellow; mouthparts light to dark brown; legs dark to light brown, femora darkest, but tarsal segments 1 and 2 yellow.

Body. Length 1.02–1.27 mm, width 0.73–0.87 mm. Elytra with long, sparse, semi-erect pubescence; punctures large, deeply impressed, and close. Metasternum convex medially with large deep close punctures laterally, smaller elsewhere on metasternum and abdominal segment 1 and shallower and sparser midposteriorly, smooth to lightly reticulate laterally. Femoral line complete, extending to three-quarters or more distance between hind coxa and posterior margin of abdominal sternite 1; area within femoral line smooth or lightly reticulate with shallow punctures. Apex of abdominal sternite 6 with deep triangular emargination in male, area around emargination concave but often with small convex bridge at apex of triangle dividing concavity in half.

Male genitalia. Siphonal capsule large knob-shaped with inner side slightly longer than outer in lateral view and divided in ventral view; sipho apex (Fig. 8) hammer shaped with outer ventral corner and inner dorsal part unpigmented, outer dorsal edge crenulate, inner ventral edge with row of teeth including 2 larger teeth at inner and outer ventral corner and often 1 large tooth near stem; apex flattened and thinner than stem of sipho in ventral view. Trabes slightly longer than tegmen, expanded distally, with proximoventral side unpigmented. Median lobe in lateral view with dorsal edge convexly curved and length more than 3 times depth; in dorsal view (Fig. 9) median lobe cleft apically with length about 2 times width. Parameres narrow and elongate, three-fifths to three-quarters length of median lobe, with ventral pores on proximal half and 0–2 pores in apical half, with 2–5 (2 long, 1 short) apical setae (in Kapur 1948, fig. 65 most apical setae should be drawn to reach or extend just beyond apex of median lobe).

Female genitalia. Most of genital plates (Fig. 10) pigmented with pores in apical half and 3–6 (5–6)

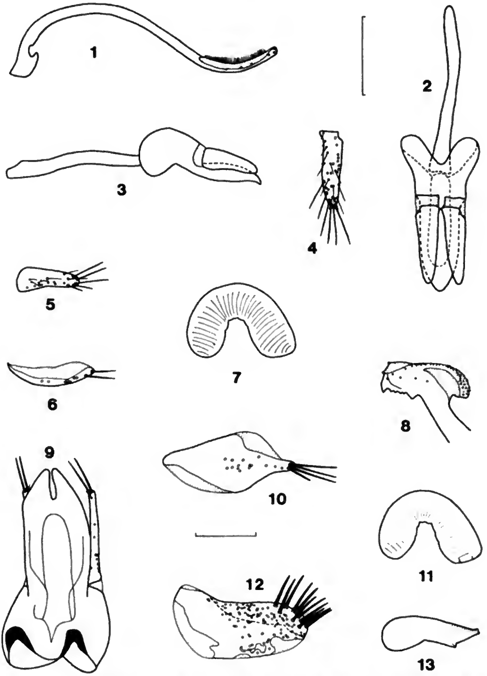

Fig. 1-13 *Stethorus*: **1–7** *S. griseus*: 1, sipho, lateral view; 2, tegmen and trabes, dorsal view; 3, tegmen and trabes, lateral view; 4, parameres, dorsal view; 5, parameres, lateral view; 6 genital plate; 7, spermatheca; **8–11** *S. bifidus*: 8, siphonal apex, lateral view; 9, tegmen, ventral view; 10, genital plate; 11, spermatheca; **12–13** *S. histrio*: 12, genital plate; 13, spermatheca (scale lines = 0.1 mm for 1–5, = 0.05 mm for 6–13). [Stipling indicates membranous areas.]

apical setae. Spermatheca (Fig. 11) annulate and C-shaped.

Last instar larva

Specimens from Nelson unpigmented; those from Waitara with anteroventral corner of head capsule below ocelli brown and dorsally with pigmentation on many setal bases with some fusion of pigment particularly on lateral half to five-eighths of meso- and metanotal plates and dorsolateral abdominal tubercles, lateral five-eighths of metanotal plate often almost completely pigmented (see Cottier 1934, fig. 1A).

Maxillary and labial palps more than twice as long as wide; long posterior setal pair on mentumnentum extending to base of anterior pair. Each tarsus with 10–12 long clavate apical setae, dorsal pair about same length as others.

e data. Holotype: New Zealand, Riwaka, 18 Jan 2, D. Miller, predacious on eggs of *Bryobia* on e. Paratypes: 5 *S. bifidus*, same data as holotype; *bifidus* and 2 *S. histrio*, New Zealand, Jan 1932, luggeridge, predacious on red spider mite; 2 *S. eus*, New Zealand. All in BMNH.

lt material examined. New Zealand. W. Cottier, lacious on *Panonychus ulmi*, 7; Jan 1932, lacious on red mite, 3.

RTH ISLAND. Palmerston North (WI) and araka (GB), 6 Dec 1931, W. Cottier, 2. **ND.** enui, Houhora Hbr, 1, (AMNZ); Mokohinau I., Broun and A. E. Brookes Collection, 1. **AK.** ia I, Noises Is, 3; Whatipu, 4; Auckland, 35; pai, Auckland, 2 Dec 1958, R. Viney, feeding on *onychus ulmi* on *Prunus persica* (L.) Batsch., 5; ban's vineyard, Henderson (NN), [Auckland], Mar 1967, *Eotetranychus sexmaculatus* (Riley) *Vitis vinifera* L., 2; New Lynn, [Auckland], 26 1953, K.P. Lamb, predator of *Tetranychus urticae* *hysalis peruviana* L., 3. **CL.** Little Barrier I, 1, INZ); Ohena I, Ohena Is, 10; Ruamahuaiti I, erman Is, 1. **WO.** Hamilton, 1. **BP.** Mamaku eau, 27 km W Rotorua, 1. **GB.** Gisborne, 1. **TK.** itara, 21 Feb 1979, N. A. Martin, predator of *anychus urticae* on *Solanum aviculare*, 19. **HB.** vkes Bay, 20 Nov 1932, Adamson, red mites on *via officinalis* L., 8; Hawkes Bay Forests Ltd, 4, NZ); Bluff Hill, Napier, 1; Hastings, 21 Aug 7, N. B. Corydon, *Tetranychus urticae* on *Malus estris*, 1; Hastings, 14; "Belmarven", Havelock th, 1. **WN.** Stokes V, Wellington, 1.

UTH ISLAND. **SD.** Stephens I, 5; Te Mahia, 27 1967, E. Collyer, pale larvae, 13; Te Mahia, 27 1967, on *Leycesteria*, pale larvae, 21, dark ae, 3. **NN.** Totaranui Saddle, 2; Riwaka Hort. Stn, 29; Nelson, 21 Mar 1921, on *Malus estris*, 9; Nelson, 4 Feb 1925, E. S. Gourlay, A. Brookes Collection, 5; Nelson, 39; Nelson orrectly labelled as Wellington], 1965, E. Collyer, es on *Malus sylvestris*, 1; DSIR Halifax St, lson], Dec 1966, E. Collyer, on *Tetranychus icae*, 1; DSIR Halifax St, [Nelson], Dec 1966, *ranychus urticae* on rose and melon, pale eggs larvae, 11; Stanton's citrus, [Nelson], Nov 1966, Collyer, on *Panonychus citri*, dark eggs, 1; Dun ack, Nelson, 19 Feb 1966, *Tetranychus urticae* on *ycesteria*, 65; Dun Track, Nelson, 10 Feb 1967, E. llyer, pale larvae, 6; Dun Track, Nelson, 10 Feb 1967, *Tetranychus urticae* on *Leycesteria*, pale larvae, 38; Mapua [W of Nelson], 1; Richmond, 18; Appleby, 28 Feb 1966, on *Tetranychus urticae* on clover delb., 11; Appleby, 1. **MB.** Blenheim, 7. **BR.** Lake Rotoiti, 1; Capleston, T. Broun and A. E. Brookes Collections, 1. **MC.** Ardagh [= Methven], 14 Feb 1912, T. Broun and A. E. Brookes Collections, 1. **CO.** Clyde R, Central Otago, 1; Alexandra, 7; Watts Rock, Carrick Ra, 2; Earnscleugh, 5.

Larval material examined. TK. Waitara, 21 Feb 1979, N. A. Martin, *Tetranychus urticae* on *Solanum aviculare*. **NN.** Dun Track, Nelson, 19 Feb 1966, *Tetranychus uticae* on *Leycesteria*, [also with *S. griseus* larvae].

Remarks. The male and female genitalia of *S. bifidus* are similar to those of the Australian *S. vagans* (Blackburn), except for the large teeth on the inner ventral edge of the siphonal apex and the longer and narrower median lobe and parameres in the male.

Stethorus histrio Chazeau

(Fig. 12, 13)

Stethorus incompletus Whitehead, 1967a: 182, 1967b: 1565. Nomen nudum.

Stethorus nigripes Kapur sensu Britton & Lee, 1972: 59 (misident.).

Stethorus histrio Chazeau, 1974: 269; Gordon & Anderson, 1979: 62; Houston, 1980: 89; Gordon & Chapin, 1983: 272.

Stethorus incompletus Chazeau, 1979: 300. New synonymy.

Adult

As described by Houston (1980) and Gordon & Chapin (1983) except: anterior third of genital plate (Fig. 12) twisted more than 90° to posterior part; spermatheca (Fig. 13) unpigmented and lightly annulate with thick cornu, long narrow nodulus, and short pointed ramus.

Last instar larva

As described by Britton & Lee (1979), Houston (1980), and Gordon & Anderson (1979).

Type data. Holotype, Stanton's citrus, [Nelson], Nov 1966, E. Collyer, *Panonychus citri*, dark eggs; another white label "*Stethorus incompletus* Whitehead 72", and a red label "*Stethorus incompletus* TYPE V.B.W. 72". Paratypes: 1, same data as holotype; 5, Nelson [incorrectly labelled as Wellington], 1965, E. Collyer, mites on apple; 1 *S. griseus*, Dun Track, Nelson, 10 Feb 1967, E. Collyer; all also with another white label "*Stethorus incompletus* Whitehead 72", and an orange label "Paratype V.B.W. 72".

Adult material examined. New Zealand. Jan 1932, predacious on red mite, 1; Jan 1932, J. Muggeridge, predacious on red spider mite, 2 (paratypes of *S. bifidus*).

NORTH ISLAND. **ND**. Kerikeri, 20 Oct 1982, U. Gerson, feeding on *Panonychus citri* on Citrus, 15; Kerikeri, 4; **AK**. Auckland, 10; **WO**. Hamilton, 2. **BP**. Katikati, 4, (FRNZ).

SOUTH ISLAND. **NN**. Nelson [incorrectly labelled as Wellington], 1965, E. Collyer, mites on *Malus sylvestris*, 1; *Stanton's citrus*, [Nelson], Nov 1966, E. Collyer, *Panonychus citri*, dark eggs, 1 (paralectotype of *S. griseus*); Nelson, 2; Whangaroa Solle, 1.

Larval material examined. ND. Kerikeri, 20 Oct 1982, U. Gerson, feeding on *Panonychus citri* on citrus.

Remarks. The presence of a spermatheca was overlooked by previous authors except Whitehead (1967a). It is membranous and easily lost during dissection and only visible on a slide under a compound microscope. Australian specimens I examined also have a spermatheca.

DISCUSSION

Nomenclature

Whitehead (1967a) described both *S. griseus* and *S. incompletus* in his thesis, available only as microfilm or xerox copies. However, this does not constitute publication within the meaning of the International Code of Zoological Nomenclature (3rd ed., 1985) as it contravenes both articles 8 and 9. The two species are noted in Whitehead (1967b) without a description but with a reference to his unpublished thesis. Since all information that affects nomenclature must be published within the meaning of the Code (article 7), *griseus* and *incompletus* are nomina nuda in Whitehead (1967a, b). Chazeau (1979) erroneously believed that the names were available and used them in a key. Since this action satisfies Article 13 of the Code, both names became available with Chazeau as their authority. Gordon & Chapin (1983) supported this interpretation.

Chazeau (1979) specifically noted that the type and paratypes of *S. incompletus* were deposited in NZAC, so that Whitehead's type series can apply directly Chazeau's *S. incompletus*. Although Chazeau did not mention the types of *S. griseus*, this species is also based on the description and therefore specimens of Whitehead (1967a); so I have here designated as lectotype the specimen labelled as type by Whitehead.

Affinities and distribution

S. griseus and *S. bifidus* are endemic to New Zealand (both with an earliest dated record of Feb 1912) and their closest relatives are in Australia, *S. nigripes* and *S. vagans*, respectively. *S. griseus* and *S. nigripes* are related to species in south-east Asia particularly *S. pauperculus* Weise and *S. parapauper-culus* Pang, whereas the genitalic characters of *S. bifidus* and *S. vagans*, show closest resemblance to those of *S. vietnamicus* Hoang from Vietnam.

S. histrio has an unusual distribution, being found on the Reunion Islands in the Indian Ocean, Australia, New Caledonia, New Zealand, Chile, and Mexico. It has been present in New Zealand since at least 1932, while the earliest Australian record is 1892 (Houston 1980). It is related to species in south-east Asia and the Pacific, particularly *S. yunnanensis* Pang & Mao, *S. guangxiensis* Pang & Mao and *S. gutierrezi* Chazeau. The Australian species *S. nigripes*, as *S. loxtoni* Britton & Lee a junior synonym, was recorded from Wellington, New Zealand [NZAC] by Chazeau (1983). He borrowed specimens from Whitehead's (1967a) type series of *S. griseus* and *S. incompletus* (R. Craw, pers. comm. 1988), but did not label any

Table 1 Tetranychid prey of *Stethorus* recorded from specimens examined.

Coccinellidae	**Tetranychidae**				
Stethorus	*Bryobia* eggs	*Eotetranychus sexmaculatus*	*Panonychus citri*	*Panonychus ulmi*	*Tetranychus urticae*
griseus			X		X
bifidus	X	X	X	X	X
histrio			X		

as *S. loxtoni*. Whitehead gave the "type locality" of both species as Wellington, but in fact all types were collected from the Nelson district (see material examined). Of the 26 types of *S. griseus* examined there were 25 *S. griseus* (1 incorrectly labelled Wellington) and 1 *S. histrio*, whereas the 8 types of *S. incompletus* included 7 *S. histrio* (5 incorrectly labelled Wellington) and 1 *S. griseus*. The only other specimens from Wellington were 2 *S. bifidus*, one of which was incorrectly labelled. There were no *S. nigripes* amongst all the material examined. Thus Chazeau's record of *S. nigripes* from New Zealand is a misidentification which cannot be attributed to a particular species.

Prey

Table 1 shows the tetranychid prey of the three *Stethorus* species noted from the specimens examined. Gordon & Chapin (1983) listed other prey records for *S. histrio*. The prey records and biological work of Cottier (1934) on "*Scymnus* sp." and Collyer (1964) on "*S. bifidus*" cannot be reliably attributed to particular species. The descriptions of the life history stages and biology of Cottier (1934) are applicable to many *Stethorus* species, except that the larva can be recognised as that of *S. bifidus*.

Identification and colour patterns of last instar larvae

S. histrio is easily recognised by its characteristic pigmentation (Britton & Lee 1972, fig. 3 as *S. nigripes* and Gordon & Anderson 1979, fig. 6), as can pigmented last instar larva of *S. bifidus* (Cottier 1934, fig. 1A as *Scymnus* sp.). Although all specimens of *S. griseus* examined were unpigmented, fresh material may show they are also characteristically pigmented. Unpigmented larvae of *S. bifidus* and *S. griseus* can be recognised by the more elongate narrower maxillary and labial palps and longer posterior setae on the mentum-submentum of *S. bifidus*, as well as differences in the number and arrangement of apical hairs on the tibio-tarsi.

Collyer (1964) noted both light and dark coloured eggs and larvae of "*S. bifidus*". However, later material from 1966 and 1967 placed by her in these categories were not conspecific. I identified the following species from it: dark eggs: *S. griseus* 1, *S. bifidus* 1, *S. histrio* 3; pale eggs: *S. bifidus* 11; dark larvae: *S. griseus* 24, *S. bifidus* 3; pale larvae: *S. griseus* 4, *S. bifidus* 89. Thus these colours are not taxonomic characters and probably depend on the internal body pigments in the prey of adults or larvae.

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I thank the curators of the institutions cited above for the loan of specimens in their care. In particular, I am grateful to Dr J. C. Watt, DSIR, Auckland, for the loan of many specimens of *Stethorus* and taxonomic advice; Dr B. A. Holloway for information on colection data; and Dr B. K. Cantrell for many helpful comments on the manuscript.

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Short Communication

Antipathes fiordensis, a new species of black coral (Coelenterata: Antipatharia) from New Zealand

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Abstract A new species of Antipatharia, *Antipathes fiordensis*, is described from the fiords of south-western New Zealand, where it is common, occurring from 4–100 m depth. It is also newly reported from Stewart Island. This species has been previously confused with and redescribed as *A. aperta* Totton but differs in details of polyps and skeletal spination.

Keywords Antipatharia; new species; fiords; Stewart Island; *Antipathes fiordensis* sp. nov.; black coral

INTRODUCTION

Grange (1988) redescribed, as *Antipathes aperta* Totton, an antipatharian black coral common throughout the fiords of south-western New Zealand, based on the similarity between the Fiordland specimens and the original description by Totton (1923). The redescription included some comments on intraspecific variability as well as illustrations of the skeletal spines and the polyps. It did not, however, include comparisons with Totton's type material which at that time was unavailable from the British Museum (Natural History).

Subsequent to that publication, paratype material of *A. aperta* was borrowed from the British Museum. This showed some differences to the Fiordland specimens, but definite conclusions could not be drawn because the material sent consisted of pinnules without fully developed skeletal spines.

During a visit to the British Museum, London, in June 1989, the holotype of *Antipathes aperta* was examined. This specimen shows clear differences in spination and in the polyps, compared to the Fiordland material, specifically in the occurrence of antler-shaped spines in the former. Although Grange's (1988) description of the Fiordland species is accurate, it is clearly not *A. aperta*. A new name is proposed here for the species.

SYSTEMATICS

Antipathes fiordensis sp. nov.

non *Antipathes aperta* Totton, 1923: Grange, 1988.

Description. In Grange (1988), as *Antipathes aperta*, with an underwater photograph of the living colony (fig. 1) and the dried skeleton (fig. 2). Colony large, up to 4.6 m tall, profusely branched, with the main stem arising from a holdfast. Pinnules 0.1–0.2 mm diameter, up to 80 mm in length, and spaced 5–10 mm apart along branchlets. Spines vary in size and shape depending on branch diameter, but are of two distinct types—primary and secondary. Primary spines on the pinnules are acicular, 0.10–0.15 mm in length and arise at angles of 40–60°. On branches greater than 1 mm in diameter, the primary spines reach a maximum length of 0.20–0.35 mm and occasionally bifurcate. Secondary spines are rarely present on pinnules, but form around the base of pinnules on branchlets and increase in frequency with branch diameter. These secondary spines are antler-shaped or irregularly branched, and 0.04–0.08 mm in length. Polyps white, arranged in a single row on one side of a branchlet or pinnule, with several rows on larger branches; width (perpendicular to branch axis) 1.0– 1.6 mm, length 0.8–1.0 mm, separated by interpolypar distances of 0.5–0.8 mm,

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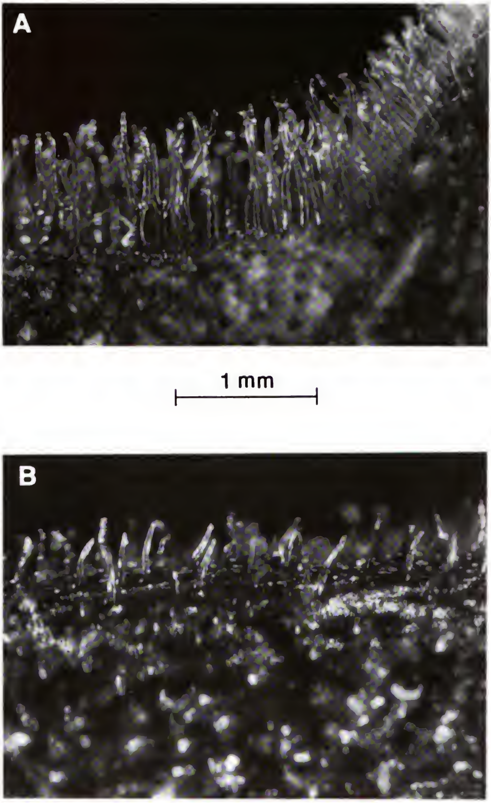

Fig. 1 Photomicrographs of 2.4 mm-diameter branches of holotypes of (A) *Antipathes aperta* and (B) *Antipathes fiordensis*.

giving 6–8 polyps per cm of branch. Fully extended, each "normal" tentacle can reach 1.2 mm in length, although most colonies produce defensive "sweeper" polyps in response to encrusting epifauna. These have greatly elongated tentacles, up to 15 mm in length, and are described elsewhere (Goldberg et al. in press).

Type data. *Antipathes fiordensis* is a large antipatharian, with colony heights exceeding 4 m. As such, it is impractical to store an entire colony as

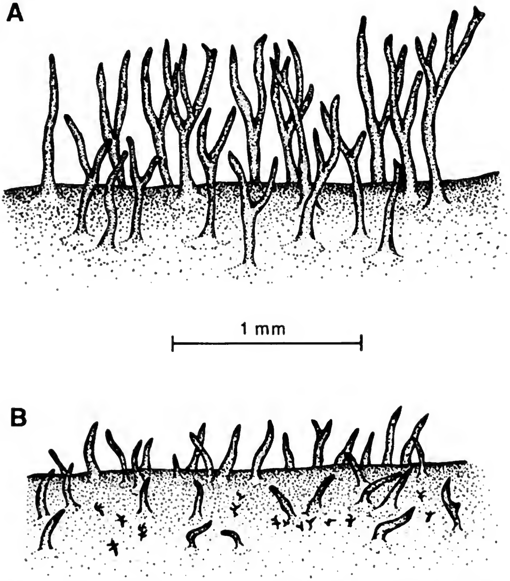

Fig. 2 (A) *Antipathes aperta* holotype showing branched primary skeletal spines. (B) *Antipathes fiordensis* holotype showing primary and secondary skeletal spines. Branches in both specimens = 2.4 mm diameter, exclusive of spines.

ble 1 Differences between the skeleton and polyps of *tipathes fiordensis* and *A. aperta*.

	A. fiordensis	*A. aperta*
nnules		
rrangement	alternate	alternate
ength	<80 mm	10–12 mm
ngle of attachment	55–60°	60–70°
istance apart	5–10 mm	2.5–3.0 mm
pines		
ength of 1°	0.20–0.35 mm	<1.1mm
ength of 2°	0.04–0.08 mm	0.04–0.08 mm
olyps		
idth	1.0–1.6 mm	0.5–0.6 mm
ength	0.8–1.0 mm	0.8 mm
umber per cm	6–8	8

a type. Therefore, two small pieces were collected from a 1.5 m tall colony growing in 15 m depth in Doubtful Sound. One piece was immediately preserved underwater to retain the shape and form of the polyps and the other had the tissue removed with a fine jet of water and was dried. **Holotype H-556**, consisting of two branches, one with polyps, the other skeleton only, deposited in the New Zealand Oceanographic Institute, DSIR, Wellington. **Paratype P-1990.3.1.1.**, a branch complete with polyps, collected from the type locality, and deposited in the British Museum (Natural History), London.

Type locality. NZOI Station O817, 45°20.95′S, 167°02.83′E. Tricky Cove, Doubtful Sound, New Zealand.

Geographic Distribution. *Antipathes fiordensis* is abundant throughout the fiords of south-western New Zealand, where it occurs from 4 m to at least 100 m depth. In November 1989, specimens were also found and collected from Port Pegasus, Stewart Island, by a Department of Conservation survey team. At this locality (NZOI Station Z6717) colonies were found at 20–30 m depth on subtidal reefs around Pearl Island, and apparently free-living (i.e., unattached to rock) on a muddy substratum in North Arm (Jane Hare, New Zealand Department of Conservation, pers. comm.).

Comparison with *Antipathes aperta* Totton. *Antipathes aperta* also has primary and secondary spines, but the primary spines branch much more commonly and profusely than in *A. fiordensis* and reach a greater length (1.1 mm). Totton's original description illustrated these spines, but the figure caption did not differentiate whether they were primary or secondary spines, and gave no scale. In shape they resemble the secondary spines of *A. fiordensis*.

Skeletal spines of the two species are compared in Fig. 1 and 2. Both illustrations are at the same magnification and from branches 2.4 mm in diameter. The specimen of *Antipathes aperta* illustrated is the holotype which could not be cut up and prepared for SEM examination, hence light micrographs and camera lucida drawings have been necessary to show the form of the spines. SEM photomicrographs of *A. fiordensis* are given in Grange (1988, fig. 3). It is obvious from these figures that the spines of *A. aperta* are considerably longer and more branched, and that secondary spines are absent at this site. By comparison, *A. fiordensis* has few branched primary spines, and secondary spines are scattered over the skeleton (Fig. 2B).

The polyps on the holotype of *Antipathes aperta* have become slightly dried out, but are considerably smaller than those of *A. fiordensis*. Totton (1923) described them as being 0.8 mm long with tentacles (contracted) 0.13 mm long. The width of the polyps on the holotype are only 0.5 mm, about half the size of those on *A. fiordensis*, so the two species may be separated by differences in spination and polyps. These are summarised in Table 1.

They may also be separated geographically. *Antipathes aperta* is known only from a depth of 129 m off North Cape, North Island, whereas *A. fiordensis* occurs around the southern coast of New Zealand in depths of 4–100 m. At present, specimens of *A. fiordensis* have been positively identified only from enclosed fiords and from an inlet on Stewart Island, but black coral is reported by fishermen to be common offshore along the Fiordland and Stewart Island coasts, so the species may be widespread around southern New Zealand.

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Short Communication

A new combination involving *Lithyphantes lepidus* Cambridge 1897 and a new name for *Teutana lepida* Cambridge 1903 (Araneae, Theridiidae)

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O. P. Cambridge described a New Zealand theridiid as *Lithyphantes lepidus* (1897, *Proceedings of the Zoological Society London*: 681–703) and a South African theridiid from Cape Town as *Teutana lepida* (1903, *Annals of the South African Museum 3 (5)*: 143–166). Since then Levi (1957, *Bulletin of the Museum of Comparative Zoology, Harvard 117*: 367–424) has recognised both *Lithyphantes* Simon 1881 and *Teutana* Thorell 1869 as junior synonyms of *Steatoda* Sundevall 1883. Following this the earlier described *L. lepidus* becomes *Steatoda lepida* new combination. As the name *S. lepida* is thus unavailable *T. lepida* requires a new name. I hereby provide the name *Steatoda capensis* nomen novum to replace *Teutana lepida* Cambridge. This name recognises the origin of the spider, that is Cape Town, South Africa.

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t Communication

ecific and general formulae for the number of d combinations for different colour-banding regimes

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tract Formulae for the number of band binations of 12 commonly used colour-banding ods are listed. In addition, general formulae for ulating the number of combinations of any od using leg-partitioning of bands are given, their use is illustrated with examples.

words Colour-bands; adjacent repeats; itioning

RODUCTION

itionally, bird banders have relied on lists of ur-band combinations to determine the number ombinations a particular regime can offer. vever, researchers can more efficiently obtain information by using mathematical formulae. is paper, I tabulate formulae for the number of ur-band combinations for 12 commonly used king regimes. These formulae can be derived general equations, which are also given below. general formulae apply to banding strategies ch involve partitioning of bands, with or without use of a metal band as one of the colours. This r extends the work of Buckley & Hancock 8) and Duncan (1972, 1987), and provides a k reference to researchers wanting to select a ding technique which optimises band and colour bers, while providing a good number of possible binations.

Description of terms

I use the term "band" to refer to both numbered metal bands and colour-coded non-metal bands; the term "colour-band" refers specifically to non-metal colour-coded bands. The 12 banding methods listed in Table 1 here use combinations of four common options available to banders. These are described below.

Adjacent repeats

An "adjacent repeat" refers to the adjacent placement of two colour-bands of the same colour in a particular combination. In most cases, the use of combinations with adjacent repeats is not recommended as it may obscure the correct banding pattern.

Partitioning

In order to increase the number of available combinations, it is often the practice to band both legs of a bird. Partitioning allows an increase in the total number of bands used. In most studies, this total remains constant, although the number of bands on each leg may vary. Calculation of the number of band combinations is made more complex if band sequences are partitioned. For this reason, the general formulae listed in this paper are specific for such studies.

Metal band present

A metal band bearing a number or code is used in addition to the colour bands. Only one such band is used, and it is often the practice to treat this band as a colour; I assume as much in this paper. However, a metal band differs from other colour bands, because it can only be used once. Consequently, formulae for calculating the number of band combinations when no metal band is used, differ from those in which a metal band is present. I give a separate general formula for calculating the number of band-combinations in the latter strategy.

Restricted numbers of bands

With partitioning, it is often desirable to restrict the number of bands on either leg to a maximum. The

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Table 1 Specific formulae for methods using the options listed. + indicates that an option is used, or as with "Adjac repeats", is allowed. The 12 methods listed here are the same as those listed by Duncan (1987).

Method No.	Adjacent repeats	Metal Band	Partitioning	Restrictions	Formulae	Constraints	References (where applicable)
1	+	–	–	–	n^r		Buckley & Hancock (196
2	–	–	–	–	$n(n-1)^{r-1}$		Duncan (1987)
3	+	+	–	–	$(r+1)n^r$		Buckley & Hancock (196
4	–	+	–	–	$n(n-1)^{r-2}[n(r+1)-2]$	$r \geq 2$	
5	+	–	+	–	$(r+1)n^r$		Duncan (1987)
6	–	–	+	–	$n(n-1)^{r-2}[n(r+1)-2]$	$r \geq 2$	
7	+	+	+	–	$(r+2)(r+1)n^r$		Duncan (1987)
8	–	+	+	–	$n(n-1)^{r-3}\{n^2(r+2)(r+1)-$ $6[n(r+1)-1]\}$	$r \geq 3$	
9	+	–	+	+	$(2s-r+1)n^r$	$s \geq r/2$	Duncan (1987)
10	–	–	+	+	$(2s-r+1)n^2(n-1)^{r-2}$	$s \geq r/2$, $r \geq 2$	
11	+	+	+	+	$(2s-r)(r+1)n^r$	$s \geq (r+1)/2$	Duncan (1987)
12	–	+	+	+	$n^2(n-1)^{r-3}(2s-r)[n(r+1)-4]$	$s \geq (r+1)/2$, $r \geq 3$	

r = total number of colour–bands per bird;
n = number of colours available; and
s = maximum number of bands per leg per bird.

Table 2 Calculations to find the number of combinations for a method with partitioning but without the use of a metal band as a colour. Adjacent repeats are excluded, and the number of bands per leg is restricted to a maximum. General formula (1) is used.

n = 5 colours
r = 6 colour-bands per bird
s = 4 bands per leg at most.
$P_x = n(n-1)^{x-1}$

use $\sum_{i=r-s}^{s} P_i \cdot P_{r-i}$

i	P_i	P_{r-i}	$P_i.P_{r-i}$
2	20	320	6400
3	80	80	6400
4	320	20	6400
			total 19200

Table 4 Calculations for the total number of combinations using 4 bands with partitioning, given the listings in Table 3a and b. General formula (2b) is used.

r = 4 colour-bands per bird
P_x is given in Table 3a for each of x bands
$P_{x/MB}$ is given in Table 3b

use 2 $\sum_{i=0}^{r} (P_i \cdot P_{r-i/MB})$

i	P_i	$P_{r-i/MB}$	$P_{i.Pr-i/MB}$
0	1	13	13
1	5	12	60
2	7	11	77
3	10	9	90
4	13	1	13
			total 253

Total number of combinations = 2 × 253 = 506

Table 3 Hypothetical listings of the number of combinations for different numbers of bands a) without partitioning and without using a metal band as a colour; and b) without partitioning but using a metal band as a colour.

a		b	
Number of bands	Number of combinations	Number of bands	Number of combinations
1	5	1	9
2	7	2	11
3	10	3	12
4	13	4	13
5	16	5	14
–	–	–	–
–	–	–	–
–	–	–	–

length of the tarsus of the bird usually restricts the number of bands to no more than three per leg, and reduces the number of combinations available.

SPECIFIC AND GENERAL FORMULAE

Table 1 gives specific formulae for the number of combinations available for each of 12 commonly-used banding methods. Of these, formulae for Methods 4, 6, 8, 10, and 12 have not been previously reported.

Methods 1 to 4 use unpartitioned sequences of bands. The formulae for these methods (and any non-partitioning banding regime) are an integral part of the general formulae for calculating the number of combinations available to any method ses partitioning with or without a metal band as our. I will state these formulae, without proof. eneral formula for the number of combinations able to a banding regime with partitioning and out a metal band is:

$$. P_{r-i} \qquad (1)$$
$$-s$$

e s=maximum number of bands per leg (s is less r); r=total number of colour-bands per bird; P_x = the number of combinations, using $x=i$ or olour-bands, available to a method with the options as the method in question, *but without tioning* (and obviously, without restriction).

he general formula for the number of binations available to a banding regime with tioning, and using a metal band as a colour is:

$$. P_i . P_{(r-i)/MB}) \qquad (2a)$$
$$r-s+1$$

n a maximum of s bands is allowed on one leg;

$$. P_i . P_{(r-i)/MB}) \qquad (2b)$$
$$0$$

n there can be as many as r colour-bands per leg. ormulae 2a and 2b, P_x = the number of binations, using $x=i$ or $r-i$ colour-bands, lable to a method with the same options as the od in question, *but without both partitioning the use of a metal band*; and P_{xMB} = the number ombinations, using $x=i$ or $(r-i)$ colour-bands, lable to a method with the same options as the hod in question, *including the use of a metal d as a colour but excluding partitioning.* all general formulae, P_0 is taken as 1.

RKED EXAMPLES

mple 1

ertain banding regime uses five colours and a l of six colour-bands per bird. However, these ds are partitioned, with the number of bands per being no more than four. No adjacent repeats are wed and a metal band is not used as a colour. m our table, this is Method 10. Using the formula n, the number of possible combinations is

$$4-6+1)\times 5^2\times 4^4 = 19\,200$$

wever, we may also use the general formula (1) to ulate the number of combinations for this method. Table 2 lays out the working for this. It is important to note that the formula used for P_i and P_{r-i} is the formula for Method 2. This method uses the same options as Method 10, except for partitioning and restriction of the number of bands per leg.

Example 2

A bird bander uses a banding regime with partitioning, and a metal band as a colour. However, the method used does not correspond to any presented in Table 1. Instead, the bander has tables of the number of combinations for two methods which are similar to the one being used except that one excludes partitioning and the use of a metal band, while the other only excludes partitioning (Table 3a and 3b; a situation such as this may arise when lists of band combinations are shared among researchers, or when certain combinations are unavailable or unacceptable. In such cases, only the number of combinations, for each set of options, are available). The bander wishes to use six colours, and only four colour-bands, without restricting the number of bands on the legs of the bird. In this case, we can use formula (2b) to calculate the number of possible combinations available. Calculations for this example are given in Table 4.

CONCLUSION

The specific formulae presented in this paper may be used to calculate the number of banding patterns for a common banding regimes. The general formulae (1) and (2), however, allow the bird-bander to calculate the banding combinations for any banding strategy.

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